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The importance of *Pratylenchus goodeyi* on bananas and plantains in the Cameroon Highlands and development of cultural controls methods

Dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Bioscience Engineering

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For Mira

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List of acronyms and abbreviations

Adj. R^2	Adjusted R^2
ANOVA	Analysis of variance
BC	Banane Cochon (*Musa* AAA, East African highland banana subgroup)
C	Organic carbon
Ca^{2+}	Calcium
CARBAP	Centre Africaine de Recherche sur Bananiers et Plantains
CSD	Cross-sectional damage
DAP	Day(s) after planting
F	Field
FAO	Food and Agriculture Organisation
FG	Essong (*Musa* AAB, plantain subgroup, type French Giant)
FRW	Fresh root weight
ha	Hectare ($=10^4$ m^2)
He	*Helicotylenchus* spp.
HG	Home garden
HIPC	Highly Indebted Poor Country
HNP	High nematode pressure
Ho	*Hoplolaimus* spp.
K^+	Potassium
LER	Leaf emission rate
LF	Relatively less fertile
LNP	Low nematode pressure
MAP	Month(s) after planting
Melo	*Meloidogyne* spp.
MF	Relatively more fertile
Mg	Megagram (= 10^6 grams = 1 tonne)
Mg^{2+}	Magnesium
MGIS	Musa Germplasm Information System
MNP	Medium nematode pressure
N	Nitrogen
NAERP	National Agricultural Extension and Research Program
n	Sample size
NDRI	Non-damaged root index
No.	Number
NSL	Number of standing leaves
P	Phosphorus
Pg	*Pratylenchus goodeyi*
PN	Petite Naine (*Musa* AAA, Cavendish subgroup)
ppm	Parts per million
rDNA	Ribosomal DNA
RNI	Root necrosis index
Rs	*Radopholus similis*
SGI	Sucker growth index
SSU	Small sub-unit
TCSD	Total cross-sectional damage (cortical and central cylinder damage)
TLA	Total leaf area
VGI	Vegetative growth index
YAP	Year(s) after planting

Summary

In Cameroon, a majority of the population depends on agriculture for their livelihood. Most agricultural products are derived from small-scale farming, with only a small fraction coming from industrial plantations. In 2001, almost half of the Cameroonian population lived below the national poverty line and most of the poor lived in rural areas. The commercialisation of food crops is therefore an important agent in poverty reduction.

On a global scale, bananas and plantains (*Musa* L. spp.) play a vital role in the food security of local populations and contribute to the economies of many developing countries. While most bananas and plantains in Cameroon are produced in the southern lowlands, the Cameroon Highlands (West and Northwest Provinces) are also an important production zone, accounting for one third of all *Musa* spp. produced in the country. The densely populated Cameroon Highlands are situated on relatively rich volcanic soils. Farms in these highlands are sometimes referred to as the 'bread basket of Cameroon'.

Plant parasitic nematodes account for severe crop damage worldwide and are recognized as a major constraint for *Musa* production. The extent of crop damage caused by nematodes depends on environmental factors, plant sensitivity and the nematode species involved. Knowledge of the relative importance of each nematode species affecting bananas and plantains is imperative when seeking effective management options, prioritising research goals or identifying technology transfer needs.

Ambient temperature is an important factor influencing nematode community species composition. In the tropical southern lowlands of Cameroon (average daily temperature 30°C), the nematode *Radopholus similis* can be found in high numbers in *Musa* roots. By contrast, in the subtropical Cameroon Highlands (average daily temperature 19°C), the nematode *Pratylenchus goodeyi* is more likely to be found in high numbers in *Musa* roots as it is better adapted to cooler temperatures. Most industrial banana plantations are found in tropical regions, explaining in part why *R. similis* has received relatively more attention from researchers.

The main objective of this study was to evaluate the importance of *P. goodeyi* for *Musa* production in small-scale farmers' fields in the Cameroon Highlands and to develop cultural control measures to limit its damage. The study is comprised of three main parts. Firstly we aimed to better understand farmers' cultivation practices and pest awareness in the study area. Secondly, we aimed to evaluate the importance of *P. goodeyi* for *Musa* production in farmers' fields

in the Cameroon Highlands. And thirdly, a host range experiment was set up in order to identify crops that can be used as rotation crops or as indicators of low infestation levels of *P. goodeyi*.

Chapter 2 describes the results obtained from the survey of 216 farming households in the West and Northwest Provinces of Cameroon. From these interviews it was apparent that *Musa* spp. are one of the most important crops for a majority of farmers. An important factor explaining the marketability of many food crops, including bananas and plantains, is the reduced income from coffee, the traditional cash crop of the Cameroon Highlands.
In all fields visited, *Musa* spp. were planted in mixed cropping systems. A total of 38 different food crops were identified during the survey, and most often, 3 or more *Musa* cultivars were planted together in a field.
For the first time in Cameroon, *R. similis* was found at altitudes above 1500 m altitude (albeit at low population densities). Most farms, however, were primarily infested with *P. goodeyi*.
The most commonly cited *Musa* production constraints were damage caused by the weevil larvae, toppling and leaf necrosis. Pest awareness was strongly linked to the visibility of the pest. While most farmers were aware of the banana weevil, only few had ever heard of a nematode before. Roughly one in five farmers applied pesticides and/or used some form of treatment of planting material before planting. The most commonly used treatments prior to planting were: ash coating, pesticide application and trimming of roots. Only few farmers pared their suckers before planting and fewer still used some form of heat treatment, either with (luke) warm or boiling water. Farmers of the West Province used inorganic products in their fields more often compared with the farmers of the Northwest province.

In Chapter 3, the effect of field history was evaluated on *in vitro* plantlets of 'Banane Cochon' (*Musa* AAA, East African highland banana subgroup), 'Essong' (*Musa* AAB, plantain subgroup type French Giant) and 'Petite Naine' (*Musa* AAA, Cavendish subgroup). An old *Musa* spp. field that had been abandoned for 14 years was visually divided into three areas of equal size. Each area differed in the number of old *Musa* plants present prior to the setup of the experiment. Two areas had a persistent growth of old *Musa* plants, at a high and medium plant density respectively, and one area had no previous *Musa* plants. The roots of the old *Musa* plants were heavily infested with nematodes and *P. goodeyi* was the most prevalent species. The old mats were uprooted and left to rot in the field. The three areas were then labelled 'high nematode pressure', 'medium nematode pressure' and 'low nematode pressure' respectively, based on field history (~ the number of previous mats).

The medium and low nematode pressure fields were relatively more fertile (in terms of macro nutrients and higher pH). The high nematode pressure field was the least fertile.

At one year after planting (YAP), the growth of plants was clearly affected by differences in field history. In the high nematode pressure field, plants were shorter, had fewer leaves, a smaller circumference and fewer suckers than in the medium or low nematode pressure fields. At flowering, vegetative parameters were determined mostly by cultivar.

At 1 YAP and at flowering, higher nematode population densities and root damage indices were found for plants in the high nematode pressure field, and lowest nematode population densities and root damage indices were found in the low nematode pressure field. A higher incidence of weevil damage was also associated with higher nematode infestation.

Among the nematode species found, *P. goodeyi* was the main cause of root damage. Root health contributed significantly to the multiple regression models for bunch weights. Where *R. similis* contributed to the model, the association with root necrosis was weak, suggesting that the pathogenicity of *P. goodeyi* in the current experiment was higher than that of *R. similis*.

The effect of this root damage was a reduced yield due to toppling, lengthening of the growth cycle and a failure to establish in fields where *Musa* mats had persisted during the fallow. In virgin (for *Musa*) fallow (*i.e.* low nematode pressure field) yields were 212% higher than in the high nematode pressure field. The number of plants that toppled accumulated gradually from 18 months after planting and occurred mostly post-flowering in the medium nematode pressure field. The combination of accumulated root damage and the higher rate of flowering, and thus top-heavy bunch weight, in the medium nematode pressure field resulted in more toppled plants. Conversely, in the high nematode pressure field root damage was higher, but fewer plants had flowered and in the low nematode pressure field root health was sufficiently high to support plants that had flowered.

Damage observed during this trial, such as reduced growth, toppling and so forth, was generally higher for Essong than for the two banana cultivars, of which Petite Naine showed the best performance.

This experiment clearly demonstrated that the root damage observed was primarily caused by *P. goodeyi* and that this nematode is thus capable of causing significant damage to *Musa* plants in farmers' fields.

In Chapter 4, the host range of *P. goodeyi* was evaluated using crops previously tested in studies in East Africa and Cameroon and additional crops and cultivars that are currently planted by farmers in the Cameroon highlands. Banana was used as a susceptible reference crop. Beans and maize (cv. CMS

8704) were good hosts of *P. goodeyi*. Watermelon and onion were intermediate hosts. Maize (cv. Kasaï), taro, okra, Irish potato and sweet potato were poor hosts; while cocoyam and tomato were very poor hosts. These results confirm that *P. goodeyi* has a narrow host range, but also highlight the importance of validation trials prior to advising crops to farmers, as differences were observed among cultivars of the same crop and with the results obtained in previous studies.

Radopholus similis is commonly thought of as the most damaging of the nematode species affecting bananas and plantains. However, as was demonstrated in this study, when the environmental conditions are suboptimal for *R. similis*, other nematodes can easily take advantage of the situation. In higher altitude regions in the tropics, where the temperature is lower, *Musa* spp. naturally have a longer growth cycle. *Pratylenchus goodeyi* is adapted to these relatively lower temperatures. The high prevalence of *P. goodeyi* compared to other nematode species, its ability to build up significant populations in the presence of a preferred host over a relatively short period of time and its damage inducing capacity when plants are exposed for long enough, suggest that this nematode may play a more important role than previously thought.

Samenvatting

De bestaanszekerheid van de meerderheid van de Kameroenese bevolking berust op landbouw. De meeste landbouwproducten in Kameroen zijn afkomstig van de kleinschalige landbouw, met slechts een fractie afkomstig van industriële plantages. In 2001 leefde bijna 50% van alle Kameroenezen onder de nationale armoedegrens en de meerderheid van de armen bevond zich onder de landelijke bevolking. De verkoop van landbouwproducten is hierdoor een belangrijk middel in de strijd tegen de armoede.
Op wereldschaal spelen bananen en plantanen (*Musa* spp.) een belangrijke rol in de voedselzekerheid van de lokale bevolking en de verkoop ervan draagt bij tot de economieën van veel ontwikkelingslanden. Terwijl de meeste *Musa* spp. van Kameroen in de zuidelijke laaglanden geproduceerd worden, zijn de Cameroon Highlands (de West en Noordwest Provincies) eveneens een belangrijke productiezone: 30% van alle in Kameroen geproduceerde *Musa* spp. zijn afkomstig van deze dichtbevolkte regio. De Cameroon Highlands zijn gekend als de 'graanschuur van Kameroen'.
Plant parasitaire nematoden zijn erkend als een serieuze belemmering bij de teelt van *Musa* spp. Het niveau van de schade die zij berokkenen, hangt af van het milieu, de gevoeligheid van de plant en de soort nematode die de schade aanricht. Een goede kennis van het relatief belang van elke nematode soort die op *Musa* spp. parasiteert, is van groot belang wanneer men effectieve beheersmaatregelen kiest, onderzoeksdoelen prioritiseert of technologie-transfernoden identificeert.
Omgevingstemperatuur speelt een belangrijke rol bij de soortensamenstelling van de nematodepopulatie. In de tropische laaglanden van Kameroen (gemiddelde dagelijkse temperatuur van 30°C), zal de nematode *R. similis* vaak in grote aantallen voorkomen in de wortels van *Musa* spp. In de subtropische Cameroon Highlands (gemiddelde dagelijkse temperatuur van 19°C) echter, zal de nematode *Pratylenchus goodeyi* eerder in grote aantallen worden aangetroffen, omdat deze soort beter aangepast is aan lagere temperaturen. De meeste commerciële bananenplantages zijn in tropische regio's. Dit verklaart deels waarom er meer onderzoek werd gedaan naar de soort *R. similis*.

De hoofddoelstelling van deze studie was te evalueren welke dreiging *P. goodeyi* vormt voor *Musa* spp. productie bij kleinschalige boeren in de Cameroon Highlands. Tevens werd gezocht naar teelttechnieken die de schade aangericht door deze nematode kunnen beperken. De studie bestaat uit drie delen. Ten eerste werd het studiegebied onder de loep genomen. Ten tweede werd het

belang van *P. goodeyi* voor de *Musa*-teelt in de Cameroon Highlands geëvalueerd. Ten derde werden aan de hand van een gastheerstudie, geschikte rotatiegewassen geïdentificeerd.

In hoofdstuk 2 worden de resultaten beschreven van een enquête bij 216 boeren in de Cameroon Highlands. De resultaten duidden *Musa* spp. aan als een van de belangrijkste gewassen voor kleinschalige boeren in de Cameroon Highlands. Een belangrijke verklaring is het verminderd inkomen afkomstig van de koffieteelt, wat samenloopt met een toenemend belang van de verkoop van voedselgewassen.
Musa spp. werden altijd in een mengcultuur geplant. In het totaal werden 38 andere gewassen geïdentificeerd tijdens de enquête. In het algemeen werden 3 of meer *Musa* cultivars samen geteeld. Voor het eerst werd *R. similis* waargenomen in Kameroen op een altitude boven 1500m. Hoewel, de meeste boerderijen hoofdzakelijk besmet waren door *P. goodeyi.*
De vaakst geciteerde productiebelemmeringen waren schade aangericht door de bananensnuitkever, omvallen en bladnecrose. Kennis van ziekten die *Musa* spp. teisteren was sterk gelinkt aan de zichtbaarheid van het pestorganisme. Terwijl de meeste boeren op de hoogte waren van de bananensnuitkever en de schade die deze kan aangerichten, had weinig van de boeren ooit van een nematode gehoord. Ongeveer één op vijf boeren sproeiden pesticiden en/of behandelden hun plantmateriaal alvorens deze te planten. De vaakst gebruikte behandelingen voor aanplant waren: bedekken met as, aanbrengen van pesticiden en inkorten van de wortelen. Slechts enkele boeren ontdeden alle wortels en de buitenste laag van het rhizoom (“paring”). Weinig boeren gebruikten een vorm van warmtebehandling, met warm ofwel kokend water. Boeren van de West Provincie gebruikten vaker anorganische producten in hun veld dan boeren van de Noordwest Provincie.

In hoofdstuk 3 wordt het effect van de teeltgeschiedenis van een veld op *in vitro* planten van ‘Banane Cochon’, ‘Essong’, en ‘Petite Naine’ besproken. Een oud *Musa* spp.-experiment dat gedurende 14 jaar braak lag, werd visueel in drie gelijke kleinere velden verdeeld, rekening houdend met het aantal oude *Musa*-bomen die overbleven van het vorig experiment. Op twee van de velden groeiden er nog steeds *Musa* spp. aan een hoge en minder hoge densiteit. Op het derde veld waren er geen *Musa* spp. te bespeuren. De oude *Musa*-bomen waren fel besmet door nematoden. Alvorens het nieuw experiment aan te leggen, werden de oude *Musa*-bomen ontworteld en ter plaatse achtergelaten om in het veld te rotten. De drie velden verschilden bijgevolg in de belasting van

nematoden en werden dus genoemd “hoog-belast”, “middel-belast” en “laag-belast”, afhankelijk van het aantal oude *Musa*-bomen.
Het middel-belast en laag-belast veld waren relatief vruchtbaarder (op het gebied van macronutriënten en hogere pH waarden). Het hoog-belast veld was het minst vruchtbaar.
Een jaar na aanplant was de groei van de planten duidelijk beïnvloed door de teeltgeschiedenis. In het hoog-belast veld waren de planten korter, hadden ze minder bladeren, een kleinere omtrek en minder scheuten dan planten van de andere twee velden. Bij de bloei werden de meeste vegetatieve kenmerken hoofdzakelijk door het effect van de cultivar bepaald.
Eén jaar na aanplant en bij de bloei werd een groter aantal nematoden en meer wortelschade aangetroffen op planten in het hoog-belast veld. De minste schade en het laagste aantal nematoden werd aangetroffen in de wortels van planten in het laag-belast veld. Schade te wijten aan de bananensnuitkever werd vaak gevonden op planten die schade van nematoden vertoonden.
Multipele regressieanalyse wees *P. goodeyi* aan als de hoofdoorzaak van wortelschade tijdens dit experiment. De gezondheid van de wortels speelde tevens een belangrijke rol bij de grootte van de trossen. Waar *R. similis* een bijdrage leverde aan het model voor trosgewicht, was de invloed van deze soort op de wortelschade minimaal. Deze bevindingen duiden erop dat *P. goodeyi* mogelijk pathogener was in dit experiment dan *R. similis.*
Het effect van de door nematoden veroorzaakte wortelschade was een lagere oogst, ten gevolge van het omvallen, een langere groeicyclus en het niet groeien van planten in velden waar *Musa*-bomen waren blijven staan tijdens de periode van braaklegging. In het braakgelegen veld waar geen *Musa*-bomen hadden gestaan, was de oogst 212% hoger dan in het veld waar een hoge densiteit aan *Musa*-bomen had gestaan tijdens de braakperiode (hoog-belast veld). Het aantal planten dat omviel, nam gestaag toe in het middel-belast veld vanaf 18 maanden na aanplant en planten vielen het meest om na de bloei. De combinatie van wortelschade enerzijds en het gewicht van de tros anderszijds, leidde tot veel omgevallen bomen in het middel-belast veld. In tegenstelling hiermee vielen relatief weinig bomen om in het hoog-belast veld, waar de wortelschade weliswaar hoger was, maar minder bomen bloeiden. In het laag-belast veld hadden dan weer veel planten gebloeid, maar de wortelschade was veel minder ernstig, waardoor deze bomen niet zo snel omvielen.
Schade, zoals verminderde groei, omvallen en zo verder, manifesteerden zich sterker bij ‘Essong’ dan bij de twee bananen cultivars; van deze vertoonde ‘Petite Naine’ de beste prestatie.
Dit experiment toonde duidelijk aan dat de wortelschade voornamelijk aan *P. goodeyi* te wijten was en dat deze soort bijgevolg belangrijke schade kan

aanrichten aan de *Musa*-teelt bij kleinschalige boeren in de Cameroon Highlands.

In hoofdstuk 4, werd het gastheerbereik van *P. goodeyi* onderzocht aan de hand van een aantal gewassen die eerder getest werden in Oost-Afrika en Kameroen, alsook een aantal bijkomende gewassen en cultivars die populair zijn bij boeren in de Cameroon Highlands. De banaan cultivar 'Grande Naine' werd gebruikt als een gekende gastheer. De volgende conclusies konden getrokken worden: bonen en maïs (cv. CMS 8704) zijn goede gastheren voor *P. goodeyi*; watermeloen en ui zijn gematigde gastheren; maïs (cv. Kasaï), taro, okra, aardappelen en zoete aardappelen zijn slechte gastheren; cocoyam en tomaten zijn zeer slechte gastheren voor *P. goodeyi*. Deze resultaten bevestigen dat *P. goodeyi* een beperkt gastheerbereik heeft, maar tonen ook hoe belangrijk het is om gewassen eerst te valideren in het veld, alvorens deze op grote schaal aan boeren te adviseren, aangezien verschillen werden opgemerkt tussen cultivars van hetzelfde gewas, alsook met de resultaten uit voorgaande studies.

Radopholus similis wordt algemeen erkend als de belangrijkste nematodesoort die *Musa* spp. teistert. Met deze studie werd echter aangetoond dat andere soorten nematoden belangrijke schade aanrichten waneer de omstandigheden suboptimaal zijn voor *R. similis*. In hogergelegen gebieden in de tropen, waar de omgevingstemperaturen lager liggen, hebben *Musa* spp. van nature een langere groeicyclus. *Pratylenchus goodeyi* is aangepast aan deze lagere temperaturen. Het overwicht van *P. goodeyi* in vergelijking met andere soorten, zijn vermogen om snel in aantal toe te nemen in aanwezigheid van een goede gastheer en de schade die hij potentieel kan berokkenen, geven aan dat deze soort een belangrijker rol speelt dan voorheen gedacht.

Chapter 1: Introduction

The present study focuses on the impact of a nematode, *Pratylenchus goodeyi* Sher & Allen, 1953, on the growth and yield of bananas and plantains (*Musa* spp.)[1] in the Cameroon Highlands. The introductory chapter illustrates the context of our study, including the importance of *Musa* spp. as a tropical food crop and *Musa* production trends in Cameroon. The morphology, taxonomical position and origin of diversity of *Musa* spp. are also reviewed. For a more thorough discussion of the context of agricultural production in the Cameroon Highlands, the reader is referred to Chapter 2. The diversity and taxonomic position of nematodes is given as an introduction to those genera that parasitize *Musa* spp. Finally, the main objectives of this thesis are summarized.

1.1 Bananas and plantains

1.1.1 Production, economic importance, food security and cultural importance

Musa spp. play a vital role in the food security of local populations and contribute to the economies of many developing countries. Bananas and plantains are the world's 4th most important food crop after rice, wheat and maize (Frison and Sharrock, 1999). As an export commodity, bananas are key contributors to the economies of many low-income food-deficit countries. Bananas are the world's most exported fresh fruit in terms of volume and value (Arias *et al.*, 2003), with a global export value in 2005 estimated at almost 5 billion US$ (FAO, 2007).

In 2009, the total world production of bananas (~70%) and plantains (~30%) was almost 130 million tonnes[2] (FAO, 2010). Roughly 85% of this production is produced by small-scale farmers in developing countries, where it is mostly self-consumed or locally traded (Arias *et al.*, 2003). India accounts for 1/5th of global banana production, destined primarily for local consumption (Arias *et al.*, 2003). Approximately 1/3rd of the *Musa* production is from sub-Saharan Africa, where bananas and plantains account for 25% of the food requirements for around 70 million people (Karamura, 1999a). The highest consumers of bananas and plantains can be found in Africa: Uganda consumes the most (243 kg per person per year) and roughly 150 kg per person is consumed annually in Rwanda, Gabon and Cameroon, where bananas and plantains

[1] Bananas and plantains will alternately be referred to as *Musa* spp, and where used as an adjective, they may be referred to simply as *Musa* (i.e. *Musa* cultivation).

[2] From here on, tonnes will be referred to in the SI unit 'Mg'.

account for 12-27% of the daily calorie intake (Arias *et al.*, 2003). The fruit is considered a good source of energy (1 g=1 kcal), vitamin B1, B2, C and potassium and is low in sodium. More vitamin A is found in bananas and plantains than in most other starchy staples (Sharrock and Lusty, 2000).
Of particular importance when considering the nutritional value of bananas and plantains is the variety and preparation method (Sharrock and Lusty, 2000) as the fruits can be boiled, roasted, baked, fried, dried, pureed or eaten raw (Ngoh Newilah *et al.*, 2005). Other uses of bananas and plantains are numerous and include the burning of the peel to make soap, use of the fibres of the pseudostem to make ropes and fermentation of the pulp to make beer. The large leaves and fast growth of *Musa* spp. make them ideal for mixed cropping systems together with cash crops, such as coffee and cacao (Sharrock and Lusty, 2000; Nkendah and Akyeampong, 2003; Kennedy, 2009).
Plantains also play an important cultural role, especially in Central Africa. For example, for the Bassakata people (Democratic Republic of Congo), cassava constitutes the main staple food. However, if a family member dies, cassava is abandoned for several weeks or months during which time only plantains and yams are allowed to be consumed (Kabeya-Hanu, 1976). In southern Cameroon, plantains are often a compulsory component of meals at weddings, funerals and other family events (Tchango-Tchango *et al.*, 1999).

1.1.2 Plantain (and banana[1]) production in Cameroon

In 1976, Fongeyn concluded a study of plantain production in Cameroon by stating that “not much work appears to have been done on plantain” and that “the traditional methods of cultivation still prevail” (Fongeyn, 1976). Almost 20 years later, Temple *et al.* (1993) wrote that the supply of plantains still required further intensification to meet the demands of a growing population. In 2003, seasonal price fluctuations continued to reflect an insufficient supply to the markets (Nkendah and Akyeampong, 2003). Over the years, however, especially in the southern lowlands of Cameroon, plantain production has gradually started to increase, becoming less traditional and more market-oriented. In 1999, an estimated 60% of the plantain production was destined for local markets and regional export (Temple *et al.*, 2006).
The increased cultivation and commercialization of *Musa* spp. in southern lowland Cameroon has been attributed to population-driven technical change, supported by *Musa* research and extension efforts. Initially, from 1970-’80,

[1] Plantains have received comparatively more attention in studies about *Musa* in Cameroon than bananas. Many statements in this section concerning plantains can be extrapolated to bananas, which are also cultivated in large quantities in Cameroon. Although a large part of the banana production is destined for export to industrialized countries, a significant portion of the banana production remains on the local markets (cf. also Chapter 2).

rapid rates of urbanisation increased the demand of urban markets in Cameroon. In the 1990s a slowing of rural-to-urban migration, associated with macroeconomic structural adjustments, increased the cohort of younger farmers in rural areas[1]. A study on the intensification of horticultural crop production by Gockowski and Ndoumbe (2004), identified farmer's age and access to income from non-agricultural labour and/or cash crop production as important determinants for the likelihood to adopt innovative management practices. Younger, wealthier farmers living in high population density areas with an improved access to roads and urban centres were more likely to intensify their agricultural production (Gockowski and Ndoumbe, 2004). Similar population-driven technical change has been observed for the production of *Musa* spp. in peri-urban farms around Yaoundé (Lemeilleur *et al.*, 2003). When the opportunity for commercialisation is met with the support of research and extension services, Temple *et al.* (2006) found that participatory research[2] can further stimulate agricultural intensification.

The decision to make structural changes in a cropping system is not without risk to the farming household whose income and food depend on a succession of carefully balanced choices. Whether change implies choosing to plant different crops or altering cultivation practices, the implications of each change must be considered. The presence of alternative opportunities (such as technical innovations, alternative crops and/or new markets) can accelerate this process of change. With regards to plantains, the change from a subsistence crop to a cash crop has not always been supported by adequate changes in production techniques. For example, Temple *et al.* (1993) note that although monocropping has been adopted by some farmers, the ensuing intensification of pest and disease problems is met with a lack of training in adequate control, thus requiring further extension efforts.

Currently, Cameroon exports plantains to neighbouring countries in Central Africa, such as Gabon, the Republic of Congo and Equatorial Guinea, thus providing an important source of income for farmers (Nkendah and

[1] Following a prosperous period from 1977-'85 with high rural-urban migration, Cameroon sank into an economic crisis due to a rapid decline in export revenue from cash crops and the depletion of petroleum reserves. During this period a deterioration in urban living standards and employment opportunities was observed, slowing the rural-urban migration. In 1989, to remedy this crisis, the government of Cameroon signed a structural adjustment agreement with the World Bank and the International Monetary Fund, agreeing to reduce public spending, liberalise markets and carry out institutional reform. Food crop production was stimulated by cuts in government support for export crop production and the devaluation of the CFA franc in 1994. From 1994-'97 a reverse urban-rural migration was seen (Ndoye and Kaimowitz, 2000).

[2] The participatory approach discussed in Temple *et al.* (2006) is based on: (1) an integrated production approach triggering technical change that is compatible with current cropping and production systems, with respect to social-, economic-, environmental- and technical opportunities and constraints, (2) the dissemination of said technical change through participatory training and (3) establishment of a network of farmer experimenters.

Akyeampong, 2003). In 2002, Ivory Coast and Cameroon accounted for 98% of all exported bananas from Africa; Cameroon produced 692 886 Mg, of which 260 000 Mg (38%) were exported, mostly (83%) to Europe (Arias *et al.*, 2003). In 2009, the total production of bananas in Cameroon was estimated at 820 000 Mg, while total plantain production was almost double (1 400 000 Mg; FAO, 2010).

1.1.3 Morphology

Bananas and plantains are giant monocotyledons, lacking true secondary growth and are thus purely herbaceous. They belong to the pantropical order of the Zingiberales and are closely related to spices such as ginger (*Zingiber officinale* Roscoe), cardamom (*Elettaria cardamomum* (L.) Maton) and turmeric (*Curcuma domestica* Val.). Plants in this order, which consists of eight families, are mostly rhizomatous perennials (Sharrock, 1997).

The family of the Musaceae contains three genera: *Musella*, *Ensete* and *Musa* (including bananas and plantains) (Kress *et al.*, 2001). *Musella lasiocarpa* (Fr.) CY Wu is an endemic and rare species from southwest China, used for various purposes by the local population (Long *et al.*, 2003). *Ensete ventricosum* (Welw.) Cheesman is a staple food crop for several million people in the southern parts of Ethiopia where starch is extracted from the corm and pseudostem of pre-flowering plants and fermented to make “kocho” (Demeke, 1986 *in* Sharrock, 1997). The fruits of *E. ventricosum* are not edible (Simmonds, 1966).

Ensete reproduces through production of large-sized fertile seeds, is non-suckering and has a distinctively swollen base. In contrast, most edible *Musa* plants are sterile, produce parthenocarpic[1] (seedless) fruit and reproduce vegetatively. Wild *Ensete* (Karamura, 1999b) but no wild *Musa* species are found in Africa. In both genera large leaves with a strong midrib are characteristic. The apparent stem is built of leaf sheaths tightly packed together and therefore called a ‘pseudostem’ (Price, 1995; Sharrock, 1997; Simmonds, 1966).

The ‘corm’, is the true underground stem. It bears buds from which lateral shoots, or ‘suckers’ arise. Young suckers only just emerging through the soil surface are termed ‘peeper suckers’. As peeper suckers grow, they may develop lanceolate leaves and a large corm (‘sword suckers’), or they may develop as ‘water suckers’ which have a narrow pseudostem, broad leaves and small corm. Sword suckers are the preferred planting material (Robinson, 1995). The first harvest is called the plant crop, the second harvest is called the first ratoon crop, the third harvest is called the second ratoon crop and so on (Swennen

[1] The ability to produce fruit without pollination.

and Rosales, 1994). The morphology of plantains, and by proxy that of bananas, is illustrated in Figure 1.1.

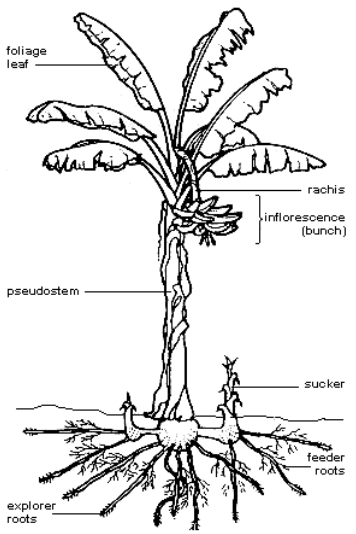

Figure 1.1: Morphology of a plantain stand (Swennen and Ortiz, 1997).

Horizontal growth of the belowground plant is slight, each shoot turning up to form a new aerial stem as soon as it is clear of the mother plant, thus forming 'mats', 'stools' or 'stands', which is the clump of plants originating from a single 'mother plant'. The largest following sucker, or selected sucker, is termed the 'ratoon sucker' and produces the bunch of the second growth cycle or 'first ratoon' (Simmonds, 1966).

Anatomically the corm is built of a central cylinder, consisting of parenchymous cells, and an outer cortex of 1-3 cm thick. As the true stem is entirely belowground, meristematic tissues for root and shoot formation are located close to one another. The meristematic region between the cortex and the central cylinder forms the roots and is also called the 'Mangin zone'. The 'apical meristem', located on the apex of the corm, forms the leaves and will eventually produce the inflorescence (Price, 1995).

Roots emerge in groups of three or four primary roots, from which secondary and tertiary roots can arise. Root growth is concentrated in the upper 50 cm of the soil and can extend up to 5 m from the mother plant, although most root growth is found within a 60 cm radius of the main stem (Price, 1995). New

cord roots are formed continuously until flowering occurs (Beugnon and Champion, 1966; Lavigne, 1987). After flowering, no new roots are formed, however, they may continue to provide nutrients for sucker development well after harvest (Blomme *et al.*, 2002).

Leaves originate at the edges of the apical meristem (Swennen and Rosales, 1994). The insertion of the leaves on the corm is circular. Initially, leaf sheaths are fully enclosing but gradually they are forced apart by the emergence of new leaves, thus widening the circumference of the plant with each following leaf that is produced. Each new leaf emerges from the centre of the pseudostem thus increasing the height of the plant.

The internodes are extremely short during vegetative growth, as the meristem does not move up much during the vegetative growth, however, at flowering the apical meristem is transformed into the 'rachis' bearing the 'inflorescence', which is pushed up through the pseudostem as internodal length increases. This flower-bearing structure is mechanically dependent on the supporting structure of the leaf sheaths and although anatomically identical to the corm has a much-reduced cortex (Simmonds, 1966; Swennen and Rosales, 1994).

The structure of the flower of *Musa* plants consists of spirally arranged flower clusters (or 'fingers' clustered in 'hands'), each protected by a deciduous bract (Sharrock, 1997). The first such clusters to appear are the female flowers that eventually form the 'bunch', which is the most commonly consumed part of the *Musa* plant. After 8-10 hands have been formed, a series of neutral flowers may be produced and, eventually, a series of male flowers. Since most fruits are phototropically positive, edible fruits exhibit a curved appearance since they turn up as soon as the bunch becomes pendulous (Swennen and Rosales, 1994). However, the appearance and formation of these structures is cultivar-dependant (Daniells *et al.*, 2001).

1.1.4 Taxonomy

Although genetic studies may eventually change the current taxonomy of bananas and plantains (Ude *et al.*, 2002; Wong *et al.*, 2002), at present the genus *Musa* consists of 30-40 species which are classified into five sections based on chromosome numbers and morphological characters: *Australimusa* (n=10)[1], *Callimusa* (n=10), *Eumusa* (n=11), *Ingentimusa* (n=14) and *Rhodochlamys* (n=11) (Ude *et al.*, 2002).

The majority of cultivated species arose from the *Eumusa* section. Therefore the *Australimusa*, *Callimusa*, *Ingentimusa* and *Rhodochlamys* sections will not be discussed further. There are 13-15 species in the *Eumusa* section but

[1] n=haploid number.

most[1] cultivated species are derived from the diploid wild ancestors of bananas, *Musa acuminata* Colla (AA) and *Musa balbisiana* Colla (BB) or a hybridisation of these two, leading to the formation of (sometimes hybrid) diploid, triploid[2] and tetraploid cultivars.

The wild ancestors originally contained many hard seeds, making them virtually inedible. Through human intervention, parthenocarpic mutants of these wild species were selected and cultivated. Female sterility, characteristic for triploid cultivars, evolved later resulting in seedless fruits even when pollinated (Simmonds, 1962 *in* Karamura, 1999b).

The terminology used to identify groups within the *Eumusa* section is based on the origin of the parents' chromosomal material (the A genome and/or the B genome) and the ploidy. For example, the triploid AAA genome (3n=33), derived solely from parent material of *M. acuminata*, designates many dessert bananas, like those of the Cavendish subgroup and also cooking bananas of the East African highland banana subgroup; the AAB genome, derived from the parent material of *M. acuminata* and *M. balbisiana*, designates dessert bananas of e.g. the Mysore subgroup and also bananas of the plantain and Maia Maoli subgroup. (Daniells *et al.*, 2001; Karamura, 1999b).

Plantains (*Musa* AAB) are further subdivided into four main 'types' depending on the morphology of the inflorescence, which exhibits a continuous spectrum of variation in its degree of degeneration (Tézenas Du Montcel *et al.*, 1983). French type plantains are characterized by a complete inflorescence, architecturally similar to that of bananas, consisting of many hermaphrodite flowers, a persistent male bud, between 6-10 hands, each with many relatively small fingers. French Horn type plantains have an incomplete inflorescence, also with many hermaphrodite flowers, but no persisting male bud, 7-8 hands and fewer but larger fingers. False Horn type plantains have an inflorescence similar to that of the French Horn type, but only few hermaphrodite flowers and less hands. And, finally, the Horn type plantains have no hermaphrodite flowers, no male bud and few hands, with few but very large fingers (Swennen *et al.*, 1995). The structure of the *Musa* flower arrangement for banana and plantain is depicted in Figure 1.2.

After identification of the genome and subgroup, the genotype or cultivar is designated, leading to, for example, the three cultivars used in Chapter 3:

[1] Although most *Musa* cultivars are derived from *M. acuminata* and *M. balbisiana*, some *Musa* cultivars have been found that derive from hybridisations with *M. schizocarpa* Simmonds (S genome) and one clone has been identified resulting from an ancient hybridization between *M. textilis* Née (T genome) and *M. balbisiana*. Additionally two landraces were identified in Papua New Guinea with three genomes: A, B and T (Daniells *et al.*, 2001).

[2] Triploid bananas generally result from the fertilization between a non-reduced diploid gamete and a haploid gamete. The diploid gametes arise accidently during meiosis when the parent genomes are too different (Perrier *et al.*, 2009).

'Banane Cochon' (*Musa* AAA, East African highland banana subgroup), 'Essong' (*Musa* AAB, plantain subgroup type French Giant[1]) and 'Petite Naine' (*Musa* spp., AAA, Cavendish subgroup) (Daniells *et al.*, 2001).

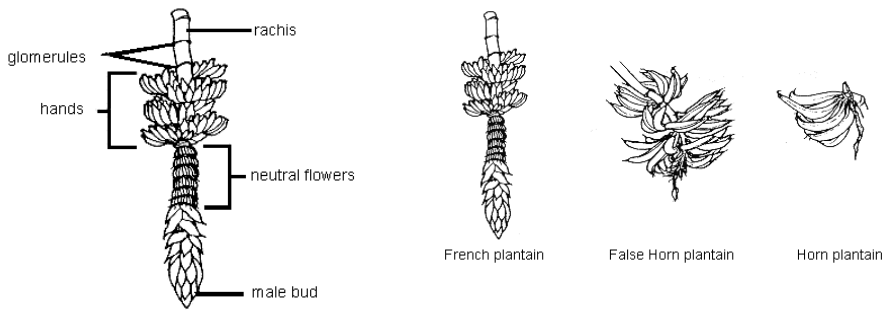

Figure 1.2: Structure of the inflorescence of bananas and plantains (Swennen and Ortiz, 1997).

1.1.4 Origin and domestication

Musa spp. are one of the oldest cultivated plants in the tropics, thought to have been domesticated in Papua New Guinea 10 000 years ago (Denham *et al.*, 2004). The centre of origin of the wild bananas stretches from India to Melanesia and from Nepal to Papua New Guinea (De Langhe, 1996; De Langhe *et al.*, 2009). A second, large diversification took place for plantain cultivars in Central Africa, from southeastern Nigeria to Gabon (Mbida *et al.*, 2001; Blench, 2009) and for East African highland banana cultivars in East Africa (De Langhe, 1996). It has been suggested that agriculture in Central Africa may have developed based on plantains (Mbida *et al.*, 2004) and that plantains assisted the Bantu expansion, by serving as a high-yielding staple that could be successfully grown in the tropical rainforest (Blench, 2009).

The botanical archaeology of bananas relies on the identification of a plant cellular structure called a "phytolith" (Vrydaghs and De Langhe, 2003). Phytoliths are silicate deposits formed either by inter- and intracellular mineralization or by the mineralization of cell walls. Unlike pollen, phytoliths are not transported far from their point of origin, persisting instead in the soil for up to 60 million years (Vrydaghs and De Langhe, 2003). Additional information on the history of *Musa* cultivation can be inferred through ethnobotanical evidence, including the diversity of the vocabulary used to refer

[1]Another aspect of *Musa* plant morphology, which is specifically used when classifying plantains, is their height: giant and medium or small (Swennen *et al.*, 1995).

to *Musa* spp. or their significance in ceremonial life, oral lore and diversity of cultural uses (Blench, 2009; Donohue and Denham, 2009; Iles, 2009). Finally, genetic evidence can provide historical information about *Musa* cultivation, as a high diversity of *Musa* spp. cultivars indicates long time cultivation and selection by local farmers (De Langhe, 2007 *in* Blench, 2009; Perrier *et al.*, 2009). For instance, the diversity and range of plantain cultivars in West and Central Africa, as well as their cultural significance, may be important indicators of their antiquity (Blench, 2009).

Archaeological, ethnobotanical and genetic evidence suggest that *Musa* spp. were transported to the East African coast across the Indian Ocean between 0-500 AD or earlier (Karamura, 1999b; Lejju *et al.*, 2006), although the exact date is disputed (Neumann and Hildebrand, 2009). Preliminary data from Cameroon indicate that farmers have been cultivating *Musa* spp. for at least 2000 years (Mbida *et al.*, 2001; Mbida *et al.*, 2004; Neumann and Hildebrand, 2009). Uncertainty remains concerning the method, transcontinental or maritime, by which plantain travelled from East to Central Africa (Lejju *et al.*, 2006; Blench, 2009).

1.2 Nematodes

1.2.1 General morphology

Nematodes are multicellular, vermiform animals. Their body length ranges from 80 µm to 8 m. Most large species are animal parasites whereas plant parasites are, in general, invisible to the naked eye. The exterior body surface consists of a cuticle. The interior organs are tubular and lie freely in a fluid-filled body cavity (pseudocoel), which is separated from the cuticle by an epidermis and functions as a hydrostatic skeleton and medium for internal transport. Body movement is sinusoidal by alternate contraction of dorsal and ventral longitudinal muscles. Unlike most metazoan animals, muscle cells extend to the nervous system, instead of the other way round, where innervation occurs. Nematodes have an alimentary, secretory-excretory and reproductive system but lack a respiratory and circulatory system relying instead on diffusion through the cuticula and movement of the body muscles for internal transport. The alimentary tract consists of a hollow tube from mouth to anus whereby the pharynx is primarily responsible for the movement of food. The ventral side is distinguished from the dorsal by the presence of an anus (cloaca in males), vulva (in females) and secretory-excretory pore. All nematodes hatch from eggs and pass through four (exceptionally three) successive juvenile stages, each separated by moulting of the cuticula. Nematodes react to mechanical, chemical and thermal stimuli with the aid of

setae or spines (sense organs), concentrated in the anterior end, around the vulva and in the tail, and paired amphids (anteriorly situated) and phasmids (posteriorly situated), which are specialized chemoreceptive structures. Photoreceptors have also been reported (Mohamed *et al.*, 2007). All external and internal stimuli are processed in a nerve ring from which radiate six longitudinal nerves connected with ganglions and bands of nerve tissue thus forming a neural net (Weischer and Brown, 2000).

1.2.2 Taxonomy, origin and evolution

Free-living nematodes live mainly in interstitial spaces in the soil and aquatic sediments but can be found almost anywhere on earth (De Ley, 2000). The extreme diversity of the phylum Nematoda reflects the ancient origin of this taxon, estimated to have evolved at least 500 million years ago. Most nematode diversity is represented by free-living nematodes, with only a fraction of the phylum parasitizing animals or plants (Baldwin *et al.*, 2004). Plant parasites, depending on the author and the order, probably evolved at least 100-130 million years ago (Baldwin *et al.*, 2004). Therefore, plant parasites were probably present when the Musaceae evolved, which has been estimated at 80 million years ago (Kress *et al.*, 2001).

The phylogeny of the phylum Nematoda has always been much debated, even more now due to the advent of molecular phylogenetic studies (*e.g.* Blaxter *et al.*, 1998; Baldwin *et al.*, 2004). The definition of a "plant parasite" can also be debated, but for the purpose of this introduction plant parasitic nematodes will be defined as nematodes that feed on plants during a portion of their life cycle (Baldwin *et al.*, 2004). Conventionally, nematode taxonomy requires many morphological and morphometric observations of specific developmental life stages. Even then, the identification and taxonomical position of nematode species is sometimes inconclusive for individual nematodes (Hooper *et al.*, 2005). Moreover, many morphological similarities among nematodes may derive from convergent evolution. The lack of an informative fossil record of nematodes makes an objective distinction between analogous and homologous structures especially difficult. By tradition, separate taxonomies were developed by nematologists who studied plant parasitic, free-living or animal parasitic nematodes, thus further confusing true phylogenetic relationships within the phylum Nematoda.

The small subunit (SSU) rDNA-based phylogeny proposed by De Ley and Blaxter (2002) is based on molecular data combined with morphological data (De Ley, 2006), thus better reflecting the phylogenetic relationships within the phylum Nematoda.

Plant parasitism is polyphyletic in origin, having arisen several times in different taxa within the phylum Nematoda. Following the classification proposed by De Ley and Blaxter (2002) and a more recent phylum-wide SSU rDNA analysis by Holterman *et al.* (2006), most plant parasitic nematodes that are important for *Musa* cultivation fall into the infra-order Tylenchomorpha, suborder Tylenchina, within the order Rhabditida. The orders Dorylaimida and Triplonchida (De Ley and Blaxter, 2002) also contain some taxa that have been found in association with *Musa* (in Cameroon), such as *Xiphinema* Cobb, 1913 and *Longidorus* (Micoletzky, 1922) Thorne & Swanger, 1936 (Bridge *et al.*, 1995) but these are of no known importance for *Musa* production.

1.2.3 Morphology and lifestyle of plant parasitic nematodes

Plant parasitic nematodes are, in general, between 0.2-1 mm in length. The digestive system consists of a pharynx, intestine, rectum and, characteristically for plant parasites, a stylet with which the nematodes suck the content of plant cells. The pharynx has two main purposes: (1) the muscular protraction and retraction of the stylet and (2) the production of species-specific glandular secretions.

The continued puncturing of cells by the stylet causes mechanical damage, whereas glandular secretions can additionally induce chemical changes in the plant cells. The chemical induction of so-called 'nurse cells' is specifically designed to nurse juvenile nematodes to maturity through an increased production and solubility of nutrients (Weischler and Brown, 2000).

Plant parasitic nematodes can feed on stems, leaves, flowers and seeds, but most are parasitic on roots. Based on the feeding strategy they are termed (1) ectoparasites: nematodes remain in the soil and do not enter the plant tissue, (2) semi-endoparasites: only the anterior part of the body enters the plant tissue or (3) endoparasites: the entire nematode penetrates the plant tissue. Further distinctions can be made between (i) sedentary nematodes and (ii) migratory nematodes. These categories are not mutually exclusive. For example, depending on the host, some species may adopt a semi-endoparasitic or ectoparasitic lifestyle (Hunt *et al.*, 2005).

1.2.3.1 Sedentary endoparasites

The females of sedentary endoparasites swell and become immobile, hence the name. Before becoming immobile, second stage juveniles (J2) are mobile and can seek out plant hosts and cells where the pharyngeal secretions induce the above mentioned 'nurse cells'. Nurse cells induced by so-called cyst nematodes

(*Heterodera* spp. Schmidt, 1871 and *Globodera* spp. Skarbilovich, 1959, not important on *Musa*) enlarge and merge, under influence of the nematode secretions, forming large multi-nuclear cells termed a 'syncytium'. Nurse cells induced by the so-called root-knot nematodes (common on *Musa*), on the other hand, enlarge and become multi-nuclear, forming a 'coenocytium' (giant cell), but do not merge with neighbouring cells. Root-knot nematodes belong to the genus *Meloidogyne* Goeldi, 1892 (family Meloidoginidae). They have a very wide host range and are sexually dimorphic. The adult females are approximately 0.3-0.7 mm wide with a slender neck. Eggs are deposited outside the body in a gelatinous matrix. J2 are slender, vermiform and about 450 µm long. The males of this genus are free-living in the soil and larger (1-2 mm; Weichsler and Brown, 2000; Hunt *et al.*, 2005).

1.2.3.2 Migratory ecto- and endoparasites

Migratory nematodes commonly found in association with the roots of *Musa* spp. include, amongst others, *Helicotylenchus* spp. (Cobb, 1893) Golden, 1956, *Hoplolaimus* spp. von Daday, 1905, *Pratylenchus* spp. Filipjev, 1936 and *Radopholus similis* Cobb, 1913. They are generally small (< 1mm-1.5mm). Reproduction is usually amphimictic (although males are rare for *R. similis*) and eggs are laid singly. Migratory plant parasitic nematodes[1] cause mechanical damage with their stylet and by burrowing through plant tissues. Secretions of the pharyngeal gland do not induce the formation of nurse cells. (Gowen *et al.*, 2005; Hunt *et al.*, 2005).

Helicotylenchus spp. and *Hoplolaimus* spp. belong to the family Hoplolaimidae and include both ecto- and endoparasitic species. The ectoparasite *Helicotylenchus dihystera* (Cobb, 1893) Sher, 1961 causes damage to the exterior root cortex (Hunt *et al.*, 2005), while *Helicotylenchus multicinctus* (Cobb, 1893) Golden, 1956, one of the few endoparasitic species within this genus, is able to complete its life cycle within the cortex, leading to more severe root damage (Gowen *et al.*, 2005). The main hosts for *Hoplolaimus pararobustus* (Schuurmans Stekhoven & Teunissen, 1938) Sher, 1963 are *Musa* spp. (CABI, 2002), however, the pathogenicity of this species remains to be evaluated (Gowen *et al.*, 2005).

Several important nematode species belonging to the family Pratylenchidae are found in association with *Musa*, suitably called the burrowing nematode (*Radopholus similis*) and the banana root lesion nematodes (*Pratylenchus coffeae* (Zimmerman, 1898) Filipjev & Schuurmans Stekhoven, 1941 and *Pratylenchus goodeyi*) (Sarah *et al.*, 1996; Bridge *et al.*, 1997). *Pratylenchus*

[1] From here onwards only plant parasitic nematodes will be considered.

spp. and *R. similis* complete their life cycle as they move through the cortex, inflicting mild or severe damage, depending on the pathogenicity of the nematode population (Fallas *et al.*, 1995). Root damage is macroscopically visible as dark red lesions, which coalesce leading to atrophy of the cortical tissue (Gowen *et al.*, 2005).

1.2.4 The importance of nematodes for banana and plantain production

The aboveground symptoms of nematode damage to bananas and plantains are related to an impaired uptake of nutrients by the plant, resulting in reduced plant growth, lengthening of the growth cycle and reduced bunch weight. The weakened root system can also lead to toppling of the plant before harvest, particularly during strong winds (Sarah *et al.*, 1996). Invasion of the central cylinder of the corm, and by homology that of the roots (termed 'stele'), is generally not observed, although they can penetrate young vascular tissue. The cortical damage they inflict may facilitate invasion by secondary fungal pathogens causing additional damage to vascular tissues (Speijer and Sikora, 1993; Pinochet, 1996; Sarah *et al.*, 1996).

Radopholus similis is one of the most damaging nematodes affecting bananas and plantains (Sarah *et al.*, 1996). Damage caused by this nematode was first observed in 1891 by Cobb on the roots of a *Musa* sp. from Fiji (Gowen *et al.*, 2005). In 1917, damage caused by *R. similis* in a commercial banana plantation was reported in Queensland, Australia (Colbran and Saunders, 1961). Through the use of infected planting material, *R. similis* became widespread in all *Musa* producing regions, where it is frequently associated with severe *Musa* yield reduction. Up to 50% yield loss due to *R. similis* has been observed in Latin America (Davide, 1996) and between 36% and 60% yield loss has been observed in Africa (Speijer and Fogain, 1999). A recent review by Price (2006), identified *R. similis* as one of the main contributing factors to banana yield decline in Uganda, where *Musa* is primarily produced as a subsistence crop by small-scale farmers. In Cameroon, Fogain (2000) found a seven-fold increase of toppling during the first ratoon of 'French Sombre' (*Musa* spp. AAB subgroup plantain type French Medium) in *R. similis*-infested plots compared to plots treated with a nematicide.

As for most tropical crops, simultaneous infection of *Musa* roots by several nematode species is common (see for instance McSorley and Parrado, 1986; Adiko, 1988; Davide, 1996; Gowen *et al.*, 2005). During a survey in Cameroon, for example, a total of 33 ectoparasitic and 13 endoparastic nematode species were identified in association with *Musa* roots (Bridge *et al.*, 1995). In the tropics at cooler temperatures (~higher altitude) and in the subtropics, *P.*

goodeyi is the more prevalent species associated with the *Musa* root system. It has been identified as a pathogen in commercial banana plantations in Australia (New South Wales), Crete and the Canary Islands (De Guiran and Vilardébo, 1962; Pattison *et al.*, 2002), but is more commonly known as a pathogen of bananas and plantains in small-scale farmers' fields in the highlands of Africa (Speijer *et al.*, 1993; Bridge *et al.*, 1995; Bridge *et al.*, 1997; Speijer and De Waele, 2001; Talwana *et al.*, 2003).

Radopholus similis and *P. goodeyi* are both endoparasitic migratory nematodes. They have both been found in comparably high numbers in *Musa* roots where they cause similar symptoms. The pathogenicity of *R. similis* has been linked to the high reproductive capacity of this species (Fallas *et al.*, 1995).

Although *P. goodeyi* has a lower reproductive capacity (Fogain, 1995; Prasad *et al.*, 1999), it is generally found in higher altitude areas. In these regions, *Musa* spp. have a longer growth cycle and hence the period for nematode population build-up (and related damage) is longer. The number of studies carried out on *P. goodeyi*, however, is very limited compared with the work that has been done on *R. similis*.

1.2.5 Nematode management

Nematode management in small-scale tropical farming systems is based on the integration of four main strategies (Bridge, 1996): (1) preventing the introduction and spread of nematodes, (2) direct non-chemical, cultural and physical control, (3) encouragement of naturally occurring control agents and (4) maintenance and enhancement of the biodiversity inherent to multiple cropping and multiple cultivar traditional farming systems to increase the available resistance or tolerance to nematodes. Nematode management options suitable for farming systems in the Cameroon Highlands will be discussed in more detail in the following chapters when they are relevant to interpret the results.

1.3 Objectives

The importance of bananas and plantains for food security is undeniable. In Cameroon, income obtained from the commercialisation of *Musa* spp. and other food crops contributes significantly to family income, complementing, and in recent years often replacing, income obtained from cash crops, such as cocoa and coffee. Although many food crops, including *Musa* spp., are produced in the Cameroon Highlands, *Musa* production in the southern lowland regions of Cameroon has received relatively more attention from researchers.

Nematode communities are diverse and concomitant infections of several nematode species are common. Knowledge of the relative importance of nematode species affecting bananas and plantains is imperative when seeking effective management options and when choosing how to prioritise research goals or identify technology transfer needs for a given region. *Radopholus similis* is a well-known *Musa* production constraint in southern lowland Cameroon. In the Cameroon Highlands[1], where altitudes are often above 1000 m, *P. goodeyi* is known to be capable of causing damage similar to that caused by *R. similis*. *Radopholus similis* has received relatively more attention from researchers however.

For these reasons, our study will focus on farming systems in the Cameroon Highlands and on *P. goodeyi*. The present study consists of the following parts:

Chapter 1

The introductory chapter discusses the context of the study and presents an outline of the main objectives.

Chapter 2

The main objectives of this chapter were to (1) achieve a better understanding of farmers' cultivation practices and pest awareness and (2) evaluate the incidence of nematode infestation at each farm visited.

Chapter 3

The main objectives of this chapter were to (1) examine the damaging potential of *P. goodeyi* and (2) compare the effect of nematode infection with the effect of edaphic and other biotic factors on growth and yield of three *Musa* cultivars.

Chapter 4

The main objective of this chapter was to examine the host range of *P. goodeyi* in order to identify crops that can be used as rotation crops or as indicators of low infestation levels of *P. goodeyi*.

Chapter 5

A summary of the key findings and their implications for research and extension in the Cameroon Highlands is discussed.

[1] In the Cameroon Highlands altitudes range between 300 – 3000 m above sea level.

Chapter 2: Cropping systems of the Cameroon Highlands: a case study of the West and Northwest Provinces of Cameroon, with emphasis on nematodes[1]

The introductory section of this chapter presents some demographic statistics of Cameroon and discusses the impact of the economic climate from 1970 to 2000 on agriculture in Cameroon. A brief introduction to the Cameroon Highlands' demography, climate, soil and land use is given to provide a context for current[2] *Musa* production in the Cameroon Highlands, which is further explored in the results section. The results of a survey (September 2002 - April 2003) discuss the most common agricultural practices and investigate farmers' perceptions of the main *Musa* production constraints and pest awareness. In order to determine which nematode species are most prevalent on *Musa* spp. in the Cameroon Highlands, a region-wide sampling of *Musa* roots was carried out at each farm visited during the survey.

2.1 Introduction

2.1.1 The demography of Cameroon

Cameroon encompasses a total area of 475 442 km². The UN Human Development Report estimated its total population in 2003 at 15.7 million, with an annual population growth of 2.6% for the period from 1975-2003 (a decrease to 1.6% is estimated for the period 2003-2015; UNDP, 2006).

Over half of the population (51.4%) are urban dwellers (EIU, 2005). Roughly 70% of the population depend on agriculture and pastoral activities for their livelihood. Small-scale farming accounts for 90% of agricultural output, with the rest coming from industrial plantations (The Economist, 2003; EIU, 2005).

A government household survey conducted in 2001 estimated that 40.2% of the population lives below the national poverty line, defined as 240 $US per

[1] Part of the results presented in this chapter have been published in:
Jacobsen K., Fogain R., Mouassom H., De Waele D. (2004): *Musa*-based cropping systems of the Cameroon Highlands: a case study of the West and Northwest provinces of Cameroon, with emphasis on nematodes. Fruits 59, 311-318.

[2] The results of the study discussed in this chapter date from 2002-2003. In May 2006, Cameroon reached the completion point for the enhanced Highly Indebted Poor Country (HIPC) initiative, allowing a debt relief of over one billion US dollars (in 1999 net present value terms). Although this debt relief will certainly impact agriculture to some extent, as it postdates the current study its potential implications are not discussed here.

person per year. Almost half the rural population lives in poverty, compared with 22% of the urban population (EIU, 2005).

2.1.2 The economic climate from 1970-2000 and its effect on agriculture in Cameroon

In a period (1970-1990) when Africa[1] on a whole was losing its share of the world market to other developing countries, which were able to produce and deliver the same goods more cheaply, Cameroon was initially still growing at a rather acceptable economic pace (Calderisi, 2006). During the decade prior to 1986, Cameroon's economy flourished, with most foreign exchange revenue coming from the export of petroleum, cocoa and coffee (Sunderlin *et al.*, 2000).

Beginning in 1986, the country faced a steep economic crisis, however, instigated by plummeting world commodity prices and diminishing petroleum reserves. Over the next few years, an overvalued currency, growing foreign debt, large-scale mismanagement, embezzlement and capital flight estimated at 1/4th of the national budget (~150 billion CFA francs), further aggravated the situation. The crisis reduced the demand from urban markets and, in combination with the overvalued exchange rate, increased the quantity of food imports to an all time high. From 1985 to 1991, producer prices of plantains, cassava and maize, fell 31, 39 and 47% respectively (Konings, 1995; Ndoye and Kaimowitz, 2000; Sunderlin *et al.*, 2000).

In 1989, following unsuccessful internal adjustment policies, the government of Cameroon signed a structural adjustment agreement with the Bretton Woods institutions (see also the footnote, page 3, Chapter 1). Among other adjustments, the government followed a policy of liberalization, which included the scrapping of the old coffee and cocoa marketing board system (EIU, 2000). Between 1990 and 1993 government subsidies for fertilizers and pesticides were reduced and eventually eliminated. Funding for research, extension and credit were also reduced during this period (Ndoye and Kaimowitz, 2000).

In 1994, Cameroon and the other CFA franc zone nations devalued the CFA franc by 50%. This currency devaluation restored much of the competitiveness of Cameroonian exports but local producers and consumers were left struggling to keep their production above subsistence levels. With the crash in cocoa and coffee prices, farmers enlarged their food crop production, as the drop in prices for food crops was less than that for coffee and cocoa (Ndoye and Kaimowitz, 2000). Thus, a decrease in food imports following the

[1] Africa refers to the 48 countries in or below the Sahara desert, excluding the five North African countries (Morocco, Algeria, Tunisia, Libya and Egypt).

devaluation of the CFA franc, stimulated local food crop production, instigating a shift away from high dependence on tree crops (cocoa and coffee) in favor of food crops, principally plantain (Sunderlin *et al.*, 2000).

2.1.3 The Cameroon Highlands: livelihoods adapted to high population pressure on rich volcanic soils

The Cameroon Highlands are situated in the West and Northwest provinces of Cameroon (Figure 2.1).

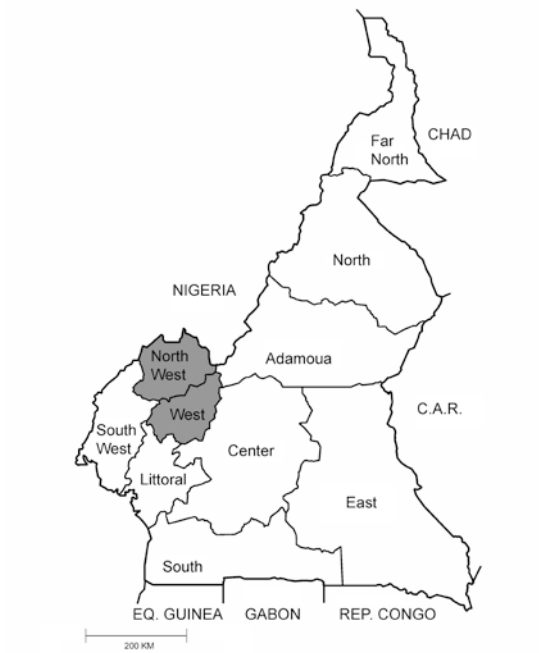

Figure 2.1: Map of the provinces of Cameroon and neighboring countries. Shaded area denotes the Cameroon Highlands.

These two provinces represent less than 10% of the total land area of Cameroon, but accommodate roughly 30% of the total population. A census carried out in 1987 showed that the Cameroon Highlands are the most densely populated region in Cameroon, with an estimated 81 inhabitants per km^2 (2 577 139 inhabitants on 31 674 km^2; Maher, 2001). Population densities range between 20 inhabitants per km^2 in the sparsest zones to above 400 inhabitants per km^2 in the densest areas, notably the Dschang Plateau (Mbapndah, 1994). Favorable agricultural conditions partly explain the high population densities

and it is estimated that the region has been continuously populated for up to 9 millennia (McHugh and Kikafunda-Twine, 1995). These high population densities lead to land shortage, as traditionally the amount of land available to any person depends on the size of the family estate and that of the family. Because of the growing population, farm plots increasingly become smaller, and part of the population has to make do with very little land, while those that do not have enough must emigrate. Land shortages have contributed to a slightly exaggerated pattern of emigration from the Cameroon Highlands toward towns and elsewhere. In fact, the Cameroon Highlands remain the area in Cameroon where the population exerts the most pressure on the land (Mbapndah, 1994).

The Cameroon Highlands are one of the main mountain systems of tropical Africa (Figure 2.2), formed of volcanic and ancient crystalline rocks (FAO, 2001). Three main soil types are found: volcanic, hydromorphic and ferralitic. The high plateaus embody rich black or brown soils, derived from basalt. The valley areas consist mainly of alluvial plains (Ministry of Information and Press - SOPECAM, 1979; Fadhani, 1998).

Figure 2.2: View of the mountains and valley around Bui, Kumbo Division, Northwest Province, Cameroon. At the forefront we see bean and taro cultivation.

Altitudes range from 300 to 3000 m above sea level. The climate is sub-tropical with low temperatures averaging 19.3 °C, although temperatures can rise above 30 °C. The rainy season, which is longer than the dry season, commences in

mid-March and lasts until mid-November. Rainfall averages 2000 mm per year (Bayemi *et al.*, 2005).

More than 25% of all plantains and 30% of all bananas produced in Cameroon are produced in the Cameroon Highlands (Fadani, 1998). Coffee cultivation was introduced during the colonial period and remains an integral, if neglected, part of many farms to this date (Mbapndah, 1994; Fadani, 1998). Due to the high human population densities, (semi-) perennial use of the farmland is common.

Free of the tsetse fly (*Glossina* spp. Wiedemann, 1830), the highlands provide an attractive setting for pastoral activities (Bayemi *et al.*, 2005), practiced mainly by the Fulani people of the so-called Bamenda Grassfields, although sedentary agriculturalists (including the Bamileke, Bamoun and many smaller Tikar groups in the Northwest) hold smaller livestock such as goats, pigs and sheep.

2.2 Objectives

The first objective of this study was to obtain a better understanding of farming practices in the Cameroon Highlands, with a strong emphasis on *Musa* cultivation practices. Farmers' perceptions of *Musa* production constraints were also documented and, in order to facilitate the implementation of integrated pest management on *Musa* spp., questions were asked about pest-awareness. The second objective was to identify the most frequently occurring endoparasitic nematode species on bananas and plantains.

The survey was carried out between September 2002 and April 2003 in close collaboration with the National Agricultural Extension and Research Program (NAERP) of Cameroon, so that conversations with farmers could be held in the local language. A brief training in paring and hot-water treatment (Colbran, 1967) was coupled with each visit. As part of a larger project, the field technicians involved in this study were later invited to the Centre Africain de Recherches sur Bananiers et Plantains (CARBAP) to attend a workshop on integrated pest management and feedback was given on the main results of the survey.

2.3 Materials and methods

The West and Northwest provinces of Cameroon can be divided into fourteen regions (region = administrative unit, cf. NAERP) of approximately equal size, whereby seven regions constitute a province. In each region, a minimum of 15 farmers were visited (216 households in total; Table 2.1).

Table 2.1: Location and number of households visited during a survey to study *Musa*-based cropping systems in the Cameroon Highlands (September 2002-April 2003).

Province	Region	Main town	Number of households visited
West Province	Bamboutos	Mbouda	15
	Haut-Nkam	Bafang	15
	Hauts-Plateaux, Mifi, Koung-Khi	Bafoussam	19
	Menoua	Dschang	15
	Nde	Bangangté	17
	Noun 1	Foumbot	15
	Noun 2	Foumban	15
Northwest Province	Boyo	Fundong	15
	Bui	Kumbo	15
	Donga Mantung	Nkambe	15
	Menchum	Wum	15
	Mezam	Bamenda	15
	Momo	Mbengwi	15
	Ngoketunijia	Ndop	15

Households were selected based on the presence of *Musa* spp. mats[1] in the fields. Field technicians of the national extension program were asked to choose farming systems representative of the farming practices applied in each region.

2.3.1 Interviews

Structured interviews were administered by the field technicians of the NAERP to farmers of the Cameroon Highlands in their local language (Annex 1). During the interviews, care was taken not to bias the answers given by the farmers. The field technicians were instructed to write down the responses literally. If a question caused silence or was obviously not understood by the farmer, the field technicians were instructed to rephrase the question as opposed to suggesting answers. After each interview, a brief report was made of the context or other remarkable information that could not be directly entered into the interview.

2.3.1.1 General

The age of the respondent and the number of people per household that depended on produce from the farm were noted. Two site types were designated: the home garden and the field, whereby the home garden was defined as a field next to the living quarters, or an area of a field that received kitchen waste, if no distinct home garden was found adjacent to the property.

[1] A mat is defined here as the clump of plants originating from a single 'mother plant'. See also section 1.1.3, Chapter 1.

Questions were asked with regard to both site types. The field technician made a visual estimation of the surface area at each site. Where this was not possible the farmer provided this information. As farms generally consist of several fields, farmers were asked in how many fields they had planted bananas and/or plantains. The altitude of the farms was estimated with a handheld altimeter.

2.3.1.2 Cultivation of bananas and plantains

Farmers were asked when they first planted *Musa* and if the plants had been planted into a fallowed area. The number of *Musa* mats in each site type was counted and an estimate of the planting density was calculated using the estimated surface area. An estimate of the number of *Musa* cultivars planted was made by noting the local names of the cultivars as given by the farmers. If a distinction was made between healthy and unhealthy suckers when plantation expansion was done, these criteria were noted. If a treatment was applied prior to planting, this too was noted.

2.3.1.3 Cropping systems, relative importance of the crops planted and food preference

All crops found in each site type were noted and farmers were asked to rank each crop in order of importance. Importance was defined as contributing significantly to the household consumption or income. *Musa* spp. were not ranked in the home gardens. In the fields, all crops including *Musa* spp. were ranked to get a comparative estimate of the importance of bananas and plantains in relation to other crops, specifically in comparison with coffee, considering the historical importance of coffee in the Cameroon Highlands. Farmers were asked if they cultivate(d) coffee and whether they (still) found it profitable. Farmers were asked to rate the importance of bananas and/or plantains particularly in relation to coffee as: less, more or equally important.
Food preferences were estimated using the following question: if the following food stuffs (plantain, cooking banana, maize, rice, Irish potato, white yam, yellow yam, cassava and taro) were placed on a table and you were free to choose, which would you prefer to eat. Subsequently farmers were asked which of these crops they ate most frequently.

2.3.1.4 Inputs

Farmers were asked to name inputs frequently used at each site type. For analysis, these inputs were grouped into two broad categories (and four subcategories): organic (manure and kitchen waste) or inorganic (fertilizers

and pesticides). Pesticides included fungicides, nematicides, insecticides and herbicides.

2.3.1.5 Constraints

The farmers were asked to describe the primary and secondary constraints for *Musa* production at each site type. An estimate was made of the distance from the field to the nearest road (to estimate the ease with which farmers had access to transport and markets, regardless of the cost of transport).

2.3.1.6 Pest awareness

Farmers were asked if they had ever heard the word “nematode” or “weevil” before. If they had, they were asked to describe what this was.

2.3.1.7 Farmer organization

Finally, farmers were asked whether they were part of a cooperative and if they had ever attended a training workshop on *Musa* cultivation techniques.

2.3.2 Sampling of the Musa root system

In the home gardens and fields, roots of bananas and plantains were sampled using the following methodology:

A total of 50 roots were sampled per site type, where possible from flowering plants. In order to account for cultivar-related susceptibility for nematode infection, as more than one *Musa* cultivar was frequently found, an equal number of roots was sampled from each cultivar. For example, if five different cultivars were planted in the field, ten roots per cultivar were sampled. When possible, more than one mat per cultivar was sampled in each site type.

On each mat sampled, a soil volume was excavated adjacent to the mother plant and the required number of roots was sampled from the root system, excluding roots close to the surface. Roots thus sampled were bulked to form one sample for each site type and for each household visited. Four home gardens and seven fields were not sampled during this survey, due to logistic difficulties. The total number of root samples collected was therefore 421.

Analyses of soil samples are usually of little value for migratory endoparasitic nematodes, such as *Radopholus similis* and *Pratylenchus goodeyi* (Sarah, 1991). For the purpose of this survey, sampling was therefore restricted to the evaluation of nematode root population densities.

2.3.3 Extraction of nematodes from roots, identification of nematode species and estimation of nematode population densities

Roots were stored in plastic bags under refrigerated conditions at 4 °C for a maximum of 1 week before extraction. In the laboratory, roots were washed in tap water and cut into 0.5 cm pieces.

From these cut roots a 50 g sub-sample was weighed and the remainder of the samples were discarded. Nematode extraction from these sub-samples was done by the maceration and sieving method (Hooper, 1990). Sub-samples were macerated in a kitchen blender with tap water. The macerated sub-sample was poured over a column of nested sieves of 200, 125, 50 and 32 µm apertures. The nematode suspensions remaining on the 50 and 32 µm aperture sieves were retained in a beaker and diluted to 100 ml with tap water.

After extraction, the root samples were cleaned through centrifugal flotation (Hooper, 1990). Five g of kaolin was added per 100 ml of nematode suspension and the mixture was centrifuged at 2500-3000 rpm. The supernatant was discarded and 15 ml of a $MgSO_4$-solution (ρ = 1.15) added to the pellet. This mixture was centrifuged during 5 min at 2500-3000 rpm. The supernatant was retained and the pellet discarded. The nematode suspension was rinsed over a 32 µm aperture sieve and diluted to 100 ml with tap water.

Per sub-sample, three 1 ml aliquots were examined. Nematodes were identified based on morphological characteristics with the aid of a stereo-microscope[1]. For counts of *Meloidogyne* spp. only second-stage juveniles (J2) were recovered using the maceration and sieving extraction method[2]. Counts of the other nematode taxa include all developmental stages. No distinction was made between male and female nematodes for any of the species found. Counts are presented as the number of nematodes per species per 100 g fresh root weight (FRW).

2.3.4 Analysis

Due to the qualitative nature of the data generated during this survey, statistical analysis was restricted to frequency distributions and percentage analyses. Unless striking differences were observed between responses given by farmers of the West and Northwest provinces, results for both provinces are presented collectively. The median was used in preference over the arithmetic

[1] The following references were used for nematode species identification: Luc *et al.* (1990), Speijer and De Waele (1997) and CABI (2002). When identification was not possible locally, taxonomical verification was done in collaboration with the Nematology Unit, ARC-Plant Protection Research Institute, Queenswood, South Africa

[2] Males of *Meloidogyne* spp. were sporadically recovered using the gravitation and sieving method, but they were generally rare.

mean, as it is less susceptible to outliers. The median is defined as the value of the variable (in an ordered array) that has an equal number of items on either side of it (Sokal and Rohlf, 2001). The arithmetic mean was used only in figure 2.5, as this graph illustrates changes in the nematode species population composition with increasing altitude. ANOVA was performed to determine whether a significant difference existed in the total nematode root population densities of *Musa* plants in the home garden and field. Prior to analysis, assumptions were checked using the Levene's test and the Kolmogorov test for normality. No data transformations were necessary. The ANOVA analysis was done, and figures were made, using SPSS for Windows, Student Version 14.0 (SPSS, Chicago, Illinois, USA).

2.4 Results

2.4.1 General

The age of the respondents ranged from 22 to 80 years, with a median of 50 years. Interviews were carried out mainly (86.4%) with the husband of the family although care was taken to discuss equally with the wife (or wives) during the discussions on other crops. The median number of people dependent on produce from the farm was 11 (Figure 2.3).

Figure 2.3: Household in the Cameroon Highlands (Ndop, Northwest Province).

Two percent of the farms visited fed 50 or more people and one household had 247 dependents.
The median surface area of home gardens in the Cameroon Highlands was 420 m^2 (0.04 ha). The largest home garden visited during the survey was 4 ha. Farms generally consisted of several small fields, each with a median surface area of 0.6 ha. The largest field visited was 9 ha. These fields can be situated many kilometers apart from each other. The altitude of the farms visited ranged from 315 m to 1914 m above sea level. The median altitude was 1302 m above sea level.
At least one banana or plantain mat was found in each home garden and most farmers (90.8% of the interviewees) who planted *Musa* spp. had more than one field where bananas and/or plantains were cultivated.

2.4.2 Musa cultivation practices and cropping systems

In the West Province, 22.5% of the farmers interviewed had planted *Musa* spp. in fields previously left to fallow for at least several years. In the Northwest Province, 80% had planted *Musa* spp. into bush fallow or virgin forest. In all other fields, the bananas and plantains had been planted into already cultivated land. Seventy-five percent of the farmers had planted *Musa* spp. at least 10 years ago (median: home garden, 20 years; field, 16.5 years). In one field, bananas and plantains had reportedly been planted 100 years ago.
Mixed cropping was the most frequently encountered cropping system. Some farmers had established a mono-cropped field as a demonstration plot in collaboration with the NAERP.
Half of the farmers interviewed planted three or four *Musa* cultivars per home garden or field. In the field, 23.4% of the farmers had planted five or more *Musa* cultivars and 1% had planted eight *Musa* cultivars. The list of vernacular and common names of *Musa* cultivars is given in Annex 2. Plant associations were extremely variable among households. Some fields were well kept and regularly weeded. Other fields resembled a secondary forest, with various fruit trees, food crops and perhaps old coffee plants planted in no particular order (Figure 2.4).

Figure 2.4: Example of two fields visited in the Cameroon Highlands. Left: field in Bantoum (Nde Division, West Province), Right: field in Alim (Boyo Division, Northwest Province).

A total of 38 different crops were identified during this survey (Table 2.2). The five most frequently encountered crops planted in association with bananas and plantains in the home gardens of the Cameroon Highlands were: cocoyam (in 62% of the home gardens visited), coffee (49%), maize (41%), taro (31%) and beans (30%). In the fields, a similar combination of crops was observed: maize (in 49% of the fields visited), cocoyam (45%), beans (42%), coffee (40%) and oil palm (27%).

Table 2.2: Crops found in association with bananas and plantains in home gardens and fields of the Cameroon Highlands.

Scientific name	Common names (French/English/Pidgin, localname)
Abelmoschus esculentus (L.) Moench.	Gombo / Okra / Okra
Allium cepa L.	Onion / Onion / Onion
Allium porrum L.	Poireaux / Leek / Leek
Ananas comosus (L.) Merr.	Ananas / Pineapple / Pineapple
Arachis hypogea L.	Arachide / Groundnut / Groundnut
Brassica oleracea L.	Choux / Cabbage / Cabbage
Capsicum annum L.	Piment doux / Sweet Pepper / Sweet Pepper
Capsicum frutescens L.	Piment / Pepper / Pepper
Carica papaya L.	Papaye / Papaya / Paw paw
Citrus limon (L.) Burm. f.	Lemon / Lemon / Lemon
Citrus sinensis (L.) Osbeck	Orange / Orange / Orange
Citrullus lanatus (Thunb.) Matsum. & Nakai	Pastèque / Watermelon / Watermelon
Coffea arabica L. & *C. canephora* L.	Café / Coffee / Coffee
Cola acuminata (Pal.) Schott & Endl.	Kola / Kola / Kola
Colocasia esculenta (L.) Schott.	Taro / Taro / Ibu coco
Cucurbita maxima L.	Melon / Melon / Egusi, Agushi, Pistache
Dacryodes edulis (G. Don) HJ Lam.	Safotier / African pear / Plum, Prune
Dioscorea sp. L.	Igname / Yam / Yam
Elaeis guineensis Jacq.	Palmier à l'huile / Oil palm / Red Oya
Eucalyptus sp. L'Her.	Eucalyptus / Eucalyptus / Eucalyptus
Glycine max (L.) Merrill	Soya / Soya / Soya beans
Ipomoea batatas (L.) Lam	Patate doux / Sweet potato/Sweet potato
Lycopersicon esculentum Mill.	Tomate / Tomato / Tomato
Magnifera indica L.	Mangue / Mango / Mango
Manihot esculenta Crantz	Manioc / Cassava / Cassava
Passiflora edulis Sims	Fruit de passion / Passion fruit / Garden egg
Persea Americana Mill.	Avocat / Avocado / Pear
Phaseolus vulgaris L.	Haricot / Beans / Beans
Psidium guajava L.	Goyave / Guava / Guava
Raphia sp. P. Beauv.	Raffia / Raffia / Raffia palm
Saccharum officinarum L.	Cane à Sucre / Sugar cane / Sugar cane
Solanum nigrum L.	Amaranth / Black nightshade / Njama njama, legumes
Solanum tuberosum L.	Pomme de terre / Potato (Irish) / Irish potato
Theobroma cacao L.	Cacao / Cacao / Cacao
Vigna unguiculata (L.) Walp.	Niébé / Cow pea / Ibo beans
Xanthosoma sagittifolium (L.) Schott	Macabo / Cocoyam / Cocoyam
Zea mays L.	Maïs / Maize/ Maize
Zingiber officinale Rosc.	Gingembre / Ginger / Ginger

Most farmers made a distinction between healthy suckers and unhealthy suckers when planning plantation expansion. Most attention was given to bunch size and type, plant vigor, leaf health status and absence of weevil galleries.

Below is a compilation of the criteria used by farmers of the Cameroon Highlands, in their own words, to distinguish between healthy and unhealthy

planting material, evaluate good growth and when to uproot and plant new suckers:

> "A sucker is healthy if the leaves are fresh and green, preferably small and lanceolate. There should be about three leaves present and the height of the sucker should be around 1 m. The base should be wider than the top and have a diameter of about 20-40 cm. There should be no black spots on the roots and when you cut the roots, water should flow freely from them. In general a healthy sucker has many roots and is well anchored in the soil. There should be no traces of weevil damage on the corm and no ants around the base. If possible it is best to take suckers from a field where you used pesticides. In summary, a healthy sucker will prevent you from contaminating your field. A healthy mother plant is the essence to obtaining a healthy sucker. One can recognize a healthy mother plant as follows: The pseudostem of the mother plant should be fresh and thick. When you make an incision in this type of pseudostem, the water should flow freely. There should be around four suckers at the base, but also not too many, as this is not a good sign. The leaves should not be yellow and it's best not to take a sucker from a toppled mother plant. A healthy mother plant produces big bunches, and it's also best if the type of bunch produced is of a marketable variety. To find out when you need to replace a mat, look at the distance between petioles. If the distance is far, the mat is still healthy. When the distance becomes shorter, this is a sign that something is wrong below ground, and it is time to uproot and plant a new sucker."

More than one out of five farmers (> 43 of the 216 interviewees) used some form of treatment before planting suckers. The most commonly used treatments were: ash coating (56% of the farmers that used some form of treatment prior to planting), pesticide application (38%) and trimming of roots (24%). Only 6% pared their suckers before planting and 5% used some form of heat treatment, either with (luke) warm or boiling water.

Bananas and plantains were usually grown in between the other crops as solitary mats. In the home garden, the median plant density of bananas and plantains was twice as high as that found in the fields (800 plants/ha). In the field, the median plant density was 382 plants ha^{-1}. *Musa* plant densities ranged from less than 20 plants/ha to 2000 plants/ha. Half of the farmers planted *Musa* at a density between 129 and 678 plants/ha.

2.4.3 Inorganic and organic inputs

In combination with the treatment of planting material (or without) most farmers used additional inputs as a management strategy in the field or home garden (Table 2.3).

Table 2.3: Percentage of farmers in the Cameroon Highlands that use organic and inorganic inputs in the home garden and field.

		% of farmers that applied inputs		
		West Province	Northwest Province	Overall
Home garden	Inorganic fertilizers	35	7	19
	Pesticides	20	4	10
	Manure	50	32	40
	Kitchen waste	88	97	92
	Total	98	95	97
	N	*103*	*103*	*206*
Field	Inorganic fertilizers	53	13	33
	Pesticides	23	13	18
	Manure	22	16	19
	Kitchen waste	3	13	8
	Total	63	43	53
	N	*108*	*105*	*213*

In the West Province, 98% of the farmers used inputs in the home garden: 35% used inorganic fertilizers, 20% used pesticides, 50% used manure and 88% used kitchen waste. In the Northwest Province, 95% of the farmers used inputs in the home garden: 7% used inorganic fertilizers, 4% used pesticides, 32% used manure and 97% used kitchen waste.

In both provinces field management differed from home garden management, with more emphasis on inorganic inputs: 33% used inorganic fertilizers, 18% used pesticides, 19% used manure and 8% used kitchen waste. Farmers of the West Province used inorganic products in their fields more often (60% used inorganic fertilizers and/or pesticides) compared with the farmers of the Northwest province (26%).

All farmers used organic inputs (manure, compost or kitchen waste) in at least one of the two site types.

2.4.4 Relative importance of crops planted in association with Musa spp.

Discussions on the importance of the various crops planted in the home garden were held with both the male and female members of the household. Maize was ranked as the most important crop in the home garden by 28% of all farmers interviewed, followed by coffee (25%), cocoyam (16%) and beans

(15%). In the West Province the food crops in the home garden ranked higher than the traditional cash crop coffee, whereas in the Northwest Province 43% of the farmers identified coffee as the most important crop in the home garden[1].

In the field *Musa* spp. were ranked in comparison with the other crops. *Musa* spp. was ranked as the most important crop in the field by 43% of all farmers interviewed, followed by maize (19%) and coffee (12%). The other crops in the field were less frequently ranked as most important for household consumption or income. In the West Province, more farmers (42.5%) cited maize as the most important crop while 29.2% ranked *Musa* spp. as the most important crop. In the Northwest Province, *Musa* spp. were ranked as the number one crop in the field by the majority of farmers (65.7%). Farmers in this province often cited the dual purpose of bananas and plantains as both a cash crop and food source.

In the context of diminished income from the traditional cash crop of the Cameroon Highlands, *Musa* spp. clearly outranked coffee in importance: a total of 89% of all farmers interviewed either had coffee in their fields or used to have it in their fields. Nevertheless, 67% of the farmers found this crop to be unprofitable and were consequently switching to other crops as an alternative source of income. Eighty-one percent of the farmers ranked *Musa* spp. as more important than coffee in particular.

2.4.5 Food preference

In both provinces, maize was more frequently cited as the preferred staple (68% of the respondents in the Northwest Province and 63.8% of the respondents in the West Province). In the Northwest Province, the most frequently preferred staples after maize were: cooking banana (14.4%), cocoyam (10.3%), plantain (4.1%) and taro (3.1%). In the West Province, the preferred staples after maize were: plantain (17%), Irish potato (4.3%), taro (4.3%), yam (4.3%), cooking banana (3.2%), cassava (2.1%) and rice (1.1%).

Food preference followed consumption patterns, with maize serving as a staple more than three times a week for 83% and 91% of the farmers in the Northwest and West Province, respectively.

[1] Bananas and plantains were not ranked in the home gardens.

2.4.6 Farmer organization and constraints as perceived by farmers

Farmer organization in "Common Initiatives Groups[1]" was relatively high, with 60% of those interviewed belonging to such an organization. Only 28% of the farmers interviewed had received some form of *Musa* production training.

The four most frequently cited constraints related to nematode damage, weevil damage, leaf necrosis diseases and reduced yield (Table 2.4). One out of five farmers cited one of these constraints as of primary or secondary importance in the home garden or field.

Constraints were often similar depending on the region (data not shown). This could be an indication of the actual constraints present in the field or the focus of extension programs in a given region. For example, in the administrative division of the Noun (West Province), many farmers referred to biting ants as a major problem in their fields, whereas in the area around Bafoussam, Mbouda and Dschang, more farmers cited weevils. Constraints cited in the home gardens and fields were similar.

Market accessibility was cited by few farmers (< 2%) as a constraint within the context of *Musa* production. The estimated median distance from the most easily accessible field to the nearest road was 200 m. At 61.4% of the farms visited this distance was less than 500 m. Ten farms (3.5%) had fields at least 2 km from the nearest road. One farm was distanced 20 km from the nearest road. However, farmers would often walk considerably further to the nearest market, due to the cost of transport.

An evaluation of pest awareness indicated that of the 216 farmers interviewed, 72% were aware of weevils and could correctly describe the insect and damage caused by it. Nine percent were able to describe the damage caused by weevils, but gave an incorrect cause (often ants). Only 19% had neither heard of weevils nor recognized damage caused by them. Many farmers were aware of the tunneling damage caused by weevil larvae and many were able to describe the larvae. However few had ever seen the adult insect.

In contrast, when asked about nematodes, pest awareness was much lower. Only 15% of all farmers correctly described root necrosis symptoms when asked about nematodes, although often an incorrect cause was given (for example ants). Farmers sometimes referred to leaf necrosis as caused by nematodes. Eighty-five percent of the farmers interviewed had neither heard of nematodes nor were aware of damage caused by them.

[1] Common Initiatives Groups (CIGs) were introduced in Cameroon as part of the rural reform in the 1990's. They were initially founded as informal groups created by local people and then legalized by the government (Brown *et al.*, 2007; Oyono and Temple, 2003).

Table 2.4: Primary and secondary *Musa* production constraints as perceived by local farmers according to a survey held in the Cameroon Highlands (September 2002-April 2003).

Constraints cited by farmers	% of farmers who cited				
	As a constraint	As a primary constraint	As a secondary constraint	As a primary constraint	As a secondary constraint
		In the home garden		In the field	
Damage caused by weevil larvae	44.8	36.4	7.3	38.8	7.0
Toppling	40.2	20.9	20.9	14.0	24.8
Leaf necrosis	32.6	24.3	8.3	22.0	10.7
Reduced yield	21.9	12.1	8.7	13.1	9.8
Lack of financial resources	12.6	1.5	7.8	4.2	11.7
Plant rot (bacterial or fungal?)	8.1	6.3	2.9	6.1	0.9
Labor shortage	8.1	1.5	5.8	1.9	7.0
Fruit damage	6.4	2.9	3.9	1.9	4.2
Ants	5.0	1.0	4.9	0.9	3.3
Root necrosis	4.0	1.9	1.5	3.3	1.4
Animal destruction (pigs, goats, etc)	3.8	1.0	2.4	2.3	1.9
Soil fertility problems	3.1	1.0	2.9	0.0	2.3
Reduced plant vigor	2.1	1.0	0.5	1.4	1.4
Weeds	2.1	0.0	1.9	0.5	1.9
Others[#]	<2.0	≤1.0	<2.0	<1.0	<1.5
n	840*	206		214	

n = number of farmers who cited primary or secondary constraints in the home garden or field; *n_{Total}= number of times constraints were cited, either as a primary or secondary constraint in the home garden or field; #: other constraints cited less frequently were lack of fertilizers/manure, unspecified insect damage, theft, high mat, soil drainage problems, premature death of the *Musa* plant, lack of planting materials, problems processing (cooking), market access problems.

2.4.7 Plant parasitic nematode population densities

Extractions of the roots sampled in the small-scale farmers' fields showed all bananas and plantains in both home gardens and fields to be infected with nematodes, ranging from low infestation (< 500 plant parasitic nematodes per 100 g FRW) to severely infested (> 100 000 nematodes per 100 g FRW). Table 2.5 shows the frequency of occurrence and abundance of the plant-parasitic nematode species extracted from *Musa* roots in home gardens and fields of the Cameroon Highlands.

Table 2.5: Plant-parasitic nematodes found in the roots of *Musa* mats in home gardens and fields in the Cameroon Highlands (September 2002-April 2003).

Species	Frequency of occurrence (%)	Maximum*	Median*	
			HG	F
Meloidogyne spp.	97.3	93 400	934	800
Pratylenchus goodeyi	91.2	114 134	5733	4800
Hoplolaimus pararobustus	78.4	3 433	200	200
Helicotylenchus multicinctus	25.7	48 400	0	0
Radopholus similis	14.9	3 734	0	0
Helicotylenchus dihystera	14.7	4 266	0	0
Helicotylenchus variocaudatus[§]	1.7	Not applicable	-	

[§]:*Helicotylenchus variocaudatus* was found in two samples; *nematodes per 100 g fresh root weight; n= 421 (home gardens and field combined); HG: Home garden; F: Field.

The most frequently occurring species were (in order of frequency): *Meloidogyne* spp., *Pratylenchus goodeyi, Hoplolaimus pararobustus, Helicotylenchus multicinctus, Radopholus similis, Helicotylenchus dihystera* and *Helicotylenchus variocaudatus* (Luc, 1960) Fortuner, 1984. Overall, the most abundant species were *P. goodeyi* (median population density: 5733 nematodes per 100 g FRW in the home garden and 4800 nematodes per 100 g FRW in the field) and *Meloidogyne* spp. (median population density: 934 nematodes per 100g FRW in the home garden and 800 nematodes per 100 g FRW in the field). *Hoplolaimus pararobustus* was extracted frequently from the roots of *Musa* mats but at lower population densities (median population density: 200 nematodes per 100 g FRW in the home garden and field). In more than half (64.8%) of all root samples between 10000-30000 *P. goodeyi* per 100 g FRW were extracted. Other nematode species extracted from *Musa* roots included three *Helicotylenchus* spp. and *R. similis,* however, these species were found less frequently and mostly at lower densities, giving a median population density of zero. Figure 2.5 shows the changes in the

nematode species population composition, in terms of abundance, from lower to higher altitudes.

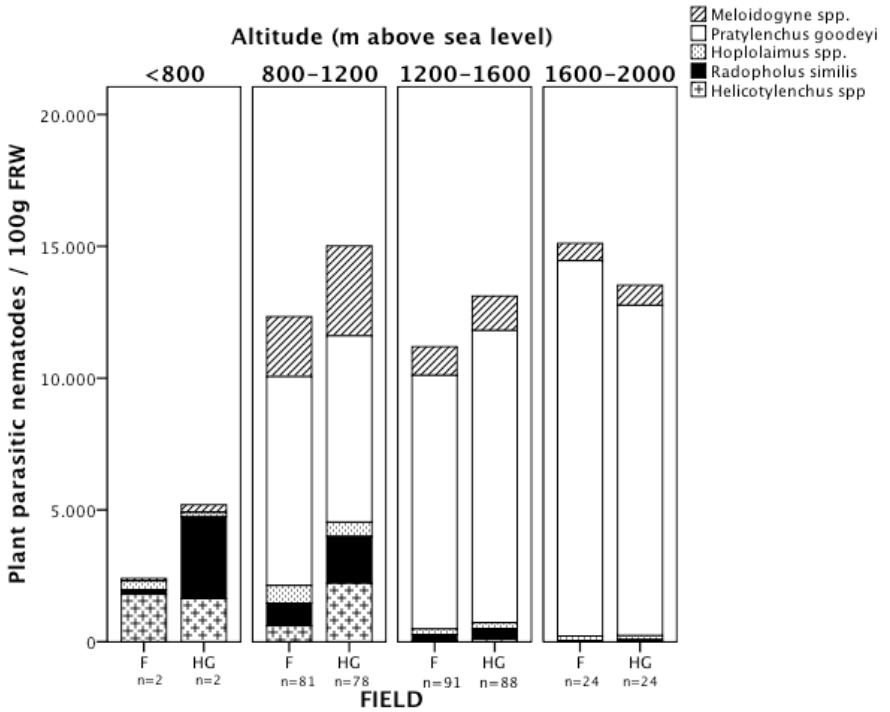

Figure 2.5: Mean[1] nematode population densities in *Musa* roots at increasing altitudes (F = Field; HG = Home garden; FRW = fresh root weight; n=390[2]).

In the home gardens and fields of the two farms located below 800 m altitude, *R. similis* was the most abundant nematode species found in the roots of *Musa* plants in the home gardens whereas *H. multicinctus* was more abundant in the roots of *Musa* plants in the field. As altitude increased, the population densities of most nematode species declined, except for *P. goodeyi* which became more abundant with increasing altitude. Whereas *R. similis* was found at 65 localities (home gardens and/or fields) in the altitude range between 800-1600 m at a mean density of 3834 *R. simils* per 100 g FRW, at altitudes higher than 1600 m *R. similis* was recovered only sporadically and at lower mean population densities (600 *R. similis* per 100 g FRW). From 800 m above

[1] Means and standard deviations are given in detail in the table in Annex 3.
[2] Sample size is reduced (n=390 instead of 421), due to missing data for altitudes of the samples taken at Dschang (altimeter was not available for that sampling mission) and at one farm in Mbouda.

sea level and higher, *P. goodeyi* was the most abundant species recovered from the roots of bananas and plantains. There was no significant difference between the nematode population densities in the roots of *Musa* plants in the home garden and those in the field.

2.5 Discussion

Bananas and plantains were most frequently cited as the most important crops for household consumption or income in the Northwest Province. For farmers in the West Province, *Musa* spp. ranked 2nd in importance after the staple crop maize. Plantain is an important component during family events, such as weddings, funerals and other celebrations (Ngoh Newilah *et al.*, 2005) and the dual purpose of bananas and plantains as a source of food and cash income (Fadani, 1998; Dury *et al.*, 2002) explains much of the importance given to these crops. Plantain is currently one of the more expensive starchy products in the urban areas in Cameroon but remains a preferred staple crop across ethnic groups (Dury *et al.*, 2002). Bananas are, in general, cheaper than plantains, making them perhaps less attractive as a source of income for small-holders. However, (cooking) bananas are frequently used in dishes throughout Cameroon and a traditional dish known as achu[1] is much appreciated in the Cameroon Highlands (Ngoh Newilah *et al.*, 2005).

The current preference of food crops as opposed to coffee confirms studies carried out in the humid forest zone of Cameroon (Ndoye and Kaimowitz, 2000; Sunderlin *et al.*, 2000), which show a trend towards increased dependency on income from food crops since the economic crisis of 1986 and the ensuing devaluation of the CFA franc.

In traditional households in the Cameroon Highlands, the agricultural roles are differentiated: men are responsible for *Musa* and coffee cultivation, livestock and palm wine. Women, on the other hand, are responsible for food crop cultivation (Fadani, 1999). During the discussions about food crops, care was taken to interview also the wife or wives of the household. For the most part, however, interviews were carried out with the husband of the family. Also, in certain regions, local custom dictates that women are not allowed to interrupt or contradict a man speaking. It is possible, therefore, that some bias is present in the answers received.

[1]The vernacular names for one of the most frequently encountered cooking bananas in the Cameroon Highlands are 'Achu banana' (Northwest Province) or 'Banane Cochon' (West Province) (Fogain, 2001). This banana is a *Musa* AAA, belonging to the East African highland banana subgroup, originally from the East African Highlands (MGIS database accessed via http://bananas.bioversityinternational.org, 2007). *Achu* is a traditional dish of the Cameroon Highlands: a starchy mixture of cooking banana and cocoyam or taro (boiled and stamped), served with a complexly spiced yellow sauce (palm oil-based) served with meat or fish (Ngoh Newilah *et al.*, 2005).

Musa and coffee trees are often found cultivated together in a plot. This is not surprising given the high degree of complementarity[1] between coffee and *Musa* spp., as well as the traditional cultivation of both crops by men. Fadani (1999) classified Arabica coffee-based farms of the Cameroon Highlands into four main types: (1) a traditional farming system consisting of mixed-cropped coffee and food crops, including livestock and palm wine tapping (58% of the farms in the Cameroon Highlands), (2) a system with dominant off-farm activities (18%), (3) a system with modern animal husbandry (15%) and (4) a system with intensive vegetable production (8%). In the system with intensive vegetable production the traditional division of labor according to gender is less strict. The vegetables are essentially grown as cash crops by the men of the household. The vegetables are mostly monocropped and with a high level of modern input use. Women assist in this cultivation, and some of the food crops are also used for household consumption. The large diversity seen in field organisation throughout the Cameroon Highlands can be viewed within the above-described context of farm typologies, as well as variability due to the cropping calendar, given that the survey was carried out over a period of 8 months.

In the selection criteria for *Musa* planting materials cited by farmers in the Cameroon Highlands, most attention was given to bunch size and type, plant vigor, leaf health status and absence of weevil galleries. In a survey carried out by Gold *et al.* (2002a), selection criteria given by small-scale farmers in Uganda were shown to depend on the destination of farm output. When *Musa* production was market-oriented, key selection criteria were bunch size and crop maturation time. When the farm output was subsistence-oriented, key selection criteria focussed on sustainability of production, such as stand longevity, and tolerance of marginal soils, although taste and crop maturation time also played a role (Gold *et al.*, 2002a).

A majority of the farmers of the Cameroon Highlands planted up to 5 different cultivars per field or home garden, with 50% planting three or four banana and/or plantain cultivars. In the East African Highlands of Rwanda and Uganda, where more than 80 cultivated varieties of locally evolved bananas are known, an average of 5.6 and as many as 22 different banana cultivars were identified per individual farm (Gold *et al.*, 2002b; Vanhoudt, 2009). The *Musa* plant density at farms in the Cameroon Highlands (382-800 mats/ha)

[1] Complementarity of coffee plants and *Musa* spp. is due to the following: (1) coffee is shade loving and *Musa* spp. are tall, so there is not much competition for light; (2) both crops are high in potassium, so coffee can benefit from the increased mulch from *Musa* leaves and other *Musa* plant debris; (3) there is a reduced need for weeding and tillage when both crops are grown together and (4) mixed-cropped coffee and *Musa* spp. plots are roughly twice as profitable compared to either crop planted as a mono-crop (Van Asten, 2010).

was generally lower than that found in Rwanda (1000-1800 mats/ha; Vanhoudt, 2009).

Musa production constraints cited by farmers during our survey focused primarily on the visibly detrimental effects of pests and diseases, such as toppling, weevil damage and leaf necrosis. Weevil damage was most frequently cited as a major constraint, supporting results obtained during a previous survey of *Musa* spp. plantations in Cameroon (Fogain, 2001) where 70% and 50% of the plantations in the West and Northwest Provinces, respectively, showed damage due to *Cosmopolites sordidus* (Germar). In studies of weevil damage in East Africa and southern lowland Cameroon, more than 30% reduced bunch weight, 17-50% higher premature death rates, toppling or snapping and lengthening of the growth cycle due to weevil damage have been reported (Rukazambuga *et al.*, 1998; Ysenbrandt *et al.*, 2000; Gold and Messiaen, 2000; Messiaen, 2002). Yield loss due to weevil damage generally becomes a bigger constraint as plantations age (Gold *et al.*, 2002c). Recognition of weevil infestation requires observations of the corm, which is exposed when plants topple or snap due to heavy infection. Many farmers interviewed during this survey knew where to look and how to identify both the weevil larvae and the related damage, although few had seen the adult insect.

Although the application of insecticides remains one of the most effective control measures for the banana weevil (Messiaen, 2002), financial constraints and the human toxicity make them prohibitive for many subsistence farmers. Other control options include the use of clean planting material (such as corm-fragment shoots), paring (to discard heavily infested suckers and remove eggs), trapping and the use of weevil-resistant cultivars or new hybrids, as many plantains and cooking bananas are highly susceptible (Gold *et al.*, 1994; Gold and Messiaen, 2000; Gold *et al.*, 2002c). In a technology transfer project in southern Cameroon, Temple *et al.* (2006) found the adoption of a technique for producing new planting materials using corm-fragment shoots to be a promising new development. This emerging new profession (nurseryman/woman) entails the production, commercialization and distribution of clean planting materials to farmers, signaling perhaps the beginning of more commercialized agricultural practices (Temple *et al.*, 2006).

Five percent of the farmers cited ants as a primary or secondary constraint in the home gardens or fields. A diagnostic survey carried out in Uganda (Gold *et al.*, 1993) reported similar concerns of ant-related damage by farmers. Although 'biting ants' are undoubtedly a nuisance, recent studies have shown that the association of some ant species is actually beneficial due to their ability to forage for weevil eggs inside the corm (Abera-Kalibata *et al.*, 2007).

Leaf necrosis on bananas and plantains is caused by one of two fungal pathogens: *Mycosphaerella fijiensis* Morelet (causing Black Sigatoka) and *M. musicola* Leach (causing Yellow Sigatoka) whereby *M. musicola* is more adapted to cooler temperatures (Mourichon *et al.*, 1997). Both *Mycosphaerella* spp. are known to cause considerable damage to bananas and plantains (Jeger *et al.*, 1995). The cost of controlling Black Sigatoka in export banana plantations is estimated at around 1000 $US per ha (Arias *et al.*, 2003). Clearly this is not an option for small-scale farmers, many of whom earn less than 240 $US per year (EIU, 2005). Leaf removal is a less costly control option and Temple *et al.* (2006) found this practice to be easily adopted by plantain producers. The reasons given by farmers for leaf removal were not always associated with control, however. The farmers cited instead: plantation cleanliness, use of leaves for food wrapping, aeration or more light for cocoa plantations (Temple *et al.*, 2006).

Nematode-related damage was frequently cited as a production constraint by farmers during this survey, but only 15% had ever heard of a nematode before.

It is not surprising that farmers were unaware of nematodes. Damage to bananas and plantains caused by nematode and weevil infection is easily confounded, as the only visible distinction requires close inspection of the roots and corm. Plant-parasitic nematodes and weevils are often found simultaneously (Sikora *et al.*, 1989; Speijer *et al;* 1993) and the exposed and damaged corm due to weevil damage may be more obvious for an untrained farmer than root necrosis. Few farmers inspected the roots of *Musa* plants for necrosis symptoms and it was also not cited frequently as a major constraint.

In the United States, Taylor (2003)[1] reported the following: “The markets for nematicides developed slowly, because [...] many farmers had never heard of nematodes and had certainly never seen any.” He went on to say that, “an educational program was needed [during the marketing of nematicides in the 1940’s and 1950’s], because the farmers were cultivating the same land for many years [...] and the old way of farming was working well, so why should they change?”.

Using demonstration plots, Taylor (2003) found that “the time from the first demonstrations in most communities [in 1946-1949], to widespread use of nematicides was about 8 years”. Thirty years later, roughly 90% of the tobacco growers in North Carolina were using nematicides, with an expected yield increase of around 35% (compared to untreated plots) (Taylor, 2003).

Although nematicides are routinely used by large banana export companies, they constitute a less suitable option for small-scale farming systems (Bridge,

[1] Reprint of a 1978 article, entitled ‘Nematocides and nematicides – a history’, originally published in the Florida Department of Agriculture Internal Information Sheet.

1996). Firstly, local farmers do not have access to the profit margin seen for exported bananas. For example, in Cameroon, the cost of a single application of (carbofuran-based) nematicide is roughly 430 US$ per ha and the resulting yield gain per effort is lower when nematicide is used to treat suckers prior to planting, compared to boiling-water treatment or hot-water treatment (Hauser, 2007). Secondly, due to their mode of action, they pose a major threat to the health of untrained users. The FAO estimates that approximately three million people are poisoned and 200,000 die from pesticide poisoning each year (FAO, 2000), with disproportionately more deaths and poisoning in developing countries. In most large cities in Cameroon, various organophosphate and organocarbamate non-fumigant nematicides can be bought over the counter (Cohan *et al.*, 2004). A survey carried out in Cameroon by Matthews *et al.* (2003) showed that most pesticides were applied without the use of protective clothing. Finally, a recent review of the environmental impact of crop protection products applied to banana plantations, identified nematicidal compounds as the most environmentally damaging compound used (before fungicides, insecticides and herbicides; Vargas, 2006).

For these reasons, nematode control measures currently advocated to small-scale *Musa* farmers in Africa focus on alternatives to nematicides, such as hot-water treatment, to obtain clean planting materials, and the use of nematode-suppressive plants like *Tithonia diversifolia* (Hemsl.) Gray as mulch (Tenkouano *et al.*, 2006). Hot-water treatment (Colbran, 1967) is the submersion of the sucker in water of 52-55°C for 20 minutes. Alternatively suckers can be dipped in boiling water for 30 seconds (Hauser, 2007). Mulch increases *Musa* yield by improving soil quality and alleviating the biotic stress imposed by nematodes (Wilson *et al.*, 1987; Rotimi, 2003). Such alternative measures allow yield gains that are comparable or even higher than those that stimulated the widespread use of nematicides by tobacco farmers in North Carolina.

All nematode species identified during this survey have previously been identified in *Musa* producing regions in Cameroon (Bridge *et al.*, 1995; Fogain, 2001). The most frequently found nematodes during this survey were *P. goodeyi* and *Meloidogyne* spp. The increasing prevalence and relative abundance of the species *P. goodeyi*[1] in samples from higher altitudes is consistent with previous reports (*e.g.* Bridge *et al.*, 1995; Price and Bridge, 1995; Fogain, 2001; Ssango *et al.*, 2004) although it is temperature rather than altitude that determines its establishment (Pattison *et al.*, 2002), as *P. goodeyi* is also found at lower altitudes in subtropical regions. More specifically, the

[1] Damage and yield loss caused by *P. goodeyi* will be more thoroughly discussed in Chapter 3.

distribution of *P. goodeyi* is influenced by the day-degree accumulations over a period of time, not simply the maximum and minimum temperatures (Bridge *et a.*, 1995). In one field a total of 114 000 nematodes per 100 g FRW of *P. goodeyi* was encountered, indicating that this species is capable of reaching high population densities.

Meloidogyne spp. were found in almost all fields visited. Stunted growth, thinner pseudostems and smaller fruit bunches of bananas caused by *Meloidogyne* spp. have been reported (Sudha and Prabhoo, 1983; Lin and Tsay, 1985; Razak, 1994). Davide and Marasigan (1985) and Brentu *et al.* (2004) observed yield reductions ranging from 26 to 57%. Other studies report no yield loss or effect on growth parameters due to *Meloidogyne* infection (Adiko, 1989; Stanton, 1994).

Helicotylenchus spp. and *Hoplolaimus* spp. are well-known parasites on bananas and plantains (McSorley and Parrado, 1986; Bridge *et al.*, 1995; Gowen *et al.*, 2005). In the Cameroon Highlands, *Hoplolaimus pararobustus* was the 3rd most frequently found nematode species, after *Meloidogyne* spp. and *P. goodeyi*, in more than 75% of the samples studied. *Musa* is the main host of *H. pararobustus* (CABI, 2002), but Price (1994b) was unable to show that it was pathogenic to banana in Cameroon. *Helicotylenchus* spp. were less frequently observed during this survey. Root damage caused by *Helicotylenchus multicinctus* has been reported (McSorley and Parrado, 1986; Davide, 1996; Chau *et al.*, 1997; Moens *et al.*, 2006) and yield reductions ranging from 19 to 34% have been observed (Parvatha Reddy, 1994; Speijer and Fogain, 1999; Brentu *et al.*, 2004). *Helicotylenchus dihystera* causes superficial root lesions and has often been reported in association with *Musa* roots (Kashaija *et al.*, 1994; Speijer *et al.*, 2001a; Pathau *et al.*, 2004). *Helicotylenchus variocaudatus* was extracted sporadically from the root samples. This species has been found previously on roots of plantain in Cameroon (Bridge *et al.*, 1995) and on cooking bananas in Rwanda (Van den Berg *et al.*, 2003). No known effect of this nematode species on bananas or plantains has been documented.

Radopholus similis was found in less than 15% of the samples examined and at relatively low population densities compared to *P. goodeyi*. *Radopholus similis* has not previously been reported at altitudes higher than 1000 m altitude in Cameroon. Price and Bridge (1995) identified an upper limit of 900 m (along a transect on Mount Cameroon) and Fogain (2001) identified *R. similis* at an altitude between 800 and 1000 m on Mount Fébé (Yaoundé, Cameroon). In the current survey, *R. similis* was found, albeit at very low population densities, at an elevation surpassing those previously reported (> 1600m). In East Africa, *R. similis* has also been identified at altitudes above 1500 m in

Tanzania (Sikora *et al.*, 1989). Below 20°C, multiplication rates of *R. similis* are greatly reduced and below 15 °C only a few European populations of *R. similis* collected from ornamental plants are able to reproduce (Elbadri *et al.*, 2001). Temperatures in the Cameroon Highlands average 19.3 °C (Ministry of Information and Press – SOPECAM, 1979; Fadani, 1998). These previous reports on the distribution of *R. similis* in Cameroon (Price and Bridge, 1995; Fogain, 2001) focused less intensively on farming systems of the Cameroon Highlands. Although it is possible that infected suckers were imported from lower altitudes and that *R. similis* population densities will decline as they are less adapted to the cooler temperatures associated with higher altitudes, it seems more likely that the upper limit of *R. similis* resembles more closely that found in East Africa.

The duration that a host plant has been planted in a field has implications with respect to pest population build-up (Freckman and Caswell, 1985; Matson *et al.*, 1997). In the Cameroon Highlands, *Musa* spp. had been planted on average 16,5 years ago in the field and 20 years ago in the home garden. Soil disturbance associated with the cultivation of annual crops has a negative effect on nematode population densities. Thomas (1978) compared the effect of different tillage regimes on nematode population densities on maize. He found highest nematode population densities in the no-till ridge plots and lowest densities in the spring- and fall-plowed plots (Thomas, 1978). While no information was gathered concerning tillage practices in the Cameroon Highlands, similar crops were grown in the home gardens and fields, suggesting that tillage regimes were most likely also similar. In this context it might be expected that nematode population densities did not differ significantly in the home gardens and fields.

Inputs in the home gardens of the Cameroon Highlands were primarily of organic origin (kitchen waste and manure) compared with the fields, where inorganic inputs were more frequently applied. The use of organic matter is known to improve plant growth, by improving nutrient content and water holding capacity of the soil and by increasing the tolerance of plants to nematode infection (Bridge, 1996). It is the beneficial effect of this difference in input management, which may explain the preference of farmers to plant *Musa* spp. in the home garden, where plant density was twice as high as that found in the field, despite similar nematode infestation levels. Plantain in particular is commonly considered to be more productive in home gardens than in fields (Wilson *et al.*, 1987).

More than half of the farmers in the West Province used inorganic inputs in their fields, whereas less than 1/3rd used inorganic inputs in the Northwest Province. A similar discrepancy between the two provinces was observed in the

use of specialized equipment for coffee production, with a more intensive use of coffee technology in the West Province compared to the Northwest Province (Fadani, 1999). No conclusive data was found to explain this difference between the two provinces. Organic inputs were widely applied in both provinces and many reports of pig-manure application to banana and plantain mats were reported.

In general, pest awareness was strongly linked to visibility of the pest. This lack can have important implications with respect to pest dispersal to uninfested fields and population build-up. General training in *Musa* spp. integrated pest management would undoubtedly be beneficial.

The willingness of farmers to participate in on-farm training was high, with an overwhelming majority of the farmers interested to participate in future collaborative projects (data not shown). Although, this may have been a form of politeness, the lack of training and need to invest in future extension efforts was clearly demonstrated.

Adult literacy levels in Cameroon are high by regional standards, standing at 74% in 1998 (EIU, 2000) and more than half the farmers interviewed during this survey were part of a Common Initiatives Group. National extension projects could easily take advantage of this relatively high level of organization, especially considering that less than 1/3rd of the farmers had received any form of *Musa* production training.

Chapter 3: The effect of field history, plant parasitic nematodes and soil characteristics on growth and yield of three *Musa* cultivars in the Cameroon Highlands.

The present chapter describes the results from an observational experiment carried out from September 2003 until December 2005 at the Mbouroukou research station. A field that was previously planted to *Musa* spp. but left abandoned for 14 years served as the experimental site into which three cultivars were planted. The introductory section of this chapter gives a brief overview of known effects of fallowing as a soil fertility and pest management option. The rationale for comparing three cultivars is also discussed in the introduction. The results of this chapter are divided into two sections, whereby the first section focuses primarily on the effect of field history and cultivar and the second section gives a comparison of the relative importance of biotic and abiotic soil conditions for *Musa* productivity and root health.

3.1 Introduction

Yield decline of banana and plantain has been attributed to high pest and disease pressure, insufficient soil fertility, weed encroachment and poor management practices (Wilson *et al.*, 1987; Banful, 2000; Hauser, 2000; Price, 2006). There is also a natural decline in root and shoot vigor during subsequent cropping cycles (Blomme *et al.*, 2006).

When yield decline is severe, plantations are frequently abandoned and fields left to fallow. Fallowing is used by commercial banana plantations and small-scale farmers (Robinson, 1995; Bridge, 1996) as a means to reduce the degradation of long-term cultivation by stimulating nutrient accumulation in the aboveground biomass, improving soil physical properties through root penetration and the recovery of soil biota (Hauser and Norgrove, 2001).

The susceptibility of the successive vegetation for plant parasitic nematodes will impact the effectiveness of fallowing as a nematode management strategy (Quénéhervé *et al.*, 2005). When the practice of fallowing is used within the context of *Musa* production, destruction of the old banana plants is essential, but not without effort.

Chemical destruction of old banana mats can be done by injecting herbicide into the apical meristem of the plant. Chabrier and Quénéhervé (2003) showed

that chemical destruction reduced the number of nematode-infected plants in the following banana crop by more than 50% whereas with mechanical destruction the emergence of volunteer shoots was problematic. Chemical destruction is not reported as a practice used by small-scale farmers and the recurring effort required for mechanical destruction to be effective is labor intensive. The result in many smaller farm holdings is a persistence of old *Musa* mats in fields that are otherwise being "fallowed".

In the African Highland regions, *Pratylenchus goodeyi* forms an important component of the pathogen complex affecting bananas and plantains and this nematode has been reported in association with (severe) root damage (*e.g.* Bridge, 1988; Bridge *et al.* 1995; Jaizme-Vega and Pinochet, 1997; Fogain, 2001). Talwana *et al.* (2003) report up to 20% plants lost due to toppling under poor management and losses of 16% caused by *P. goodeyi* have been reported in Gran Canaria (Rodriguez, 1975 *in* Pinochet *et al.*, 1998).

Damage caused by nematodes is a function of the ability of a nematode species to colonize a host plant and cause disease symptoms (pathogenicity), the susceptibility of the host plant and various environmental factors which impact the plant-pathogen interaction, such as soil fertility, rainfall and drainage, diversity of the soil micro-organisms etc (Gowen, 1995; Van Asten *et al.*, 2004). Variable rates of population increase of *P. goodeyi* were observed depending on the susceptibility of the cultivar (Prasad *et al.*, 1999). Inherent variability in root system characteristics (Swennen *et al.*, 1986; Blomme *et al.*, 2000) and phenotypic traits (Osuji *et al.*, 1997) will additionally affect the tolerance of cultivars to adverse environmental conditions, such as drought (Thomas *et al.*, 1998) and the susceptibility to nematode infection (De Waele, 1996; Pinochet, 1996; Fogain and Gowen, 1998; Pinochet *et al.*, 1998).

3.2 Objectives

The general objective of the current study was to examine plant growth and yield of three *Musa* cultivars under extensive management conditions in response to varying initial population densities of *P. goodeyi* and other factors. To this end a fallowed field was chosen and divided into three equally sized areas defined by the number of previous *Musa* mats that had remained in the field during the fallow period. The specific objectives of our study are described in two separate sections.

The objectives in the first section were:

(1) to compare the actual yield with the theoretically attainable yield and to quantify the yield loss (= difference between actual and attainable yield);

(2) to partition the yield loss according to known nematode effects on *Musa* production;
(3) to examine the effect of field history and cultivar on yield and yield loss;
(4) to examine the effect of field history and cultivar on plant growth and root health parameters;

The objectives in the second section were:

(5) to estimate the relative importance of nematodes and non-nematode factors for plant growth and productivity and to delineate the effect of nematodes from non-nematode factors.

3.3 Materials and methods

3.3.1 Site, experimental design and field history

The experiment was set up at the Mbouroukou Research Station at Mbouroukou village (5°06' N, 9°89' E, Littoral Province, Cameroon). The Mbouroukou Research Station is located at 1200 m above sea level on the slopes of the Manengouba mountain range. Mount Manengouba (summit 2411 m above sea level) is a polygenic volcanic complex of the Cameroon line (Figure 3.1), which originated in the Quaternary[1] (Dongmo *et al.*, 2001).

The average daily temperature at Mbouroukou is 20 °C and the average annual rainfall is 1900 mm, with the rainy season commencing in April and ending in October. Soils are volcanic dark-brown loams with a pH of 4.9. Soils are generally deep with 80% of the soils deeper than 50 cm. The soil texture is loam with silty trends stained with darkish browns. There are few gravels of weathered basalt origins. Stones on the surface are black basalts and brown pyroclastic materials. Soils are relatively acid, but rich in plant nutrients (Sama-Lang, unpublished).

Mbouroukou is situated in a forest-savannah transition area. Fallow and weed vegetation was dominated by *Aspilia Africana* (Pers.) CD Adams, *Cyperus* spp. L., *Mariscus* spp. Vahl, *Mimosa* spp. L. and *Pennisetum* spp. Pers. A non-exhaustive list of plant species identified in the fallow prior to planting the experiment is given in Table 3.1. A more detailed analysis of soil chemical properties is given in the results section.

Fourteen years prior to the set up of this field experiment at the Mbouroukou Research Station, part of the field had been used to conduct a *Musa* experiment. Since 1989, that experiment had been abandoned (left to fallow).

[1] The Quaternary = from 2 million years ago to the present.

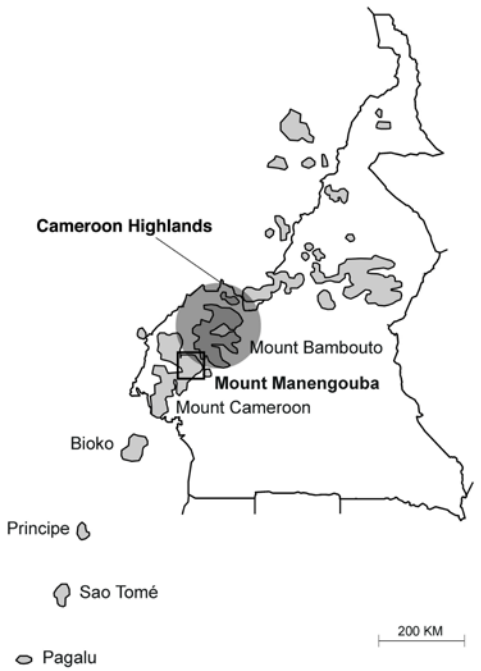

Figure 3.1: The Cameroon volcanic line: The village of Mbouroukou is located on the northeast flank of Mount Manengouba. Further northeast are the Cameroon Highlands (adapted from Dongmo *et al.*, 2001).

Table 3.1: Non-exhaustive list of plant species identified in the fallow prior to planting the experiment at Mbouroukou.

Ageratum conyzoides L.	*Kyllinga squamulata* Vahl.
Aspilia africana	*Lepianthes peltata* (L.) Raf.
Asystasia gangetica (L.) T. Anders	*Mimosa diplotricha* C. Wright ex Sauv.
Bidens pilosa L.	*Paspalum conjugatum* Berg
Centella asiatica (L.) Urban	*Phyllanthus* sp. L.
Chromolaena odorata (L.) King & Robinson	*Pueraria phaseoloides* (Roxb.) Benth.
Cleome gynandra L.	*Setaria* sp. Beauv.
Other *Cleomaceae* spp. Bercht. & J. Presl.	*Sida abutifolia* Mill.
Commelina diffusa Burm. f.	*Spilanthes filicaulis* (Schum. & Thonn.) CD Adams
Conyza sumatrensis (Retz.) Walker	*Trianthema portulacastrum* L.
Cyperus rotundus L.	*Urochloa maxima* (Jacq.) Webster
Cyathula prostrata (L.) Blume	*Vernonia* sp. Schreb.
Drymaria sp. Willd. ex Schult.	*Veronica cinerea* Boiss. & Bal.
Emilia coccinea (Sims) G. Don	*Zehneria scabra* (L.f.) Sond.

When the experiment was abandoned, no effort was made to destroy the plants and so, mats from the previous experiment persisted on the site during the 14-year period. The original layout of the old experiment was no longer visible and it was not possible to obtain information concerning the original set-up. *Musa* cultivars used in the previous experiment were identified as 'Gros Michel' (*Musa* AAA), a French Giant type plantain (*Musa* AAB) and 'Yangambi km5' (*Musa* AAA), but few of the old mats were still productive. Prior to manual slashing of the fallow vegetation and uprooting of the previous *Musa* mats, plots were pegged out in the field and labeled. The current experiment was set up as a randomized block design with three replicates of three cultivars planted randomly per block (= factor field history; cf. section 3.3.7 Data handling and statistical analysis). The blocking criterion was the plant density of previous *Musa* mats from the fallowed experiment.

Each replicate consisted of a plot of 16 *in vitro* plantlets, planted at 2 x 2 m (2500 plants/ha), with 4 m corridors between plots. The *in vitro* plantlets were produced at the *in vitro* laboratory at the Centre Africain de Recherches sur Bananiers et Plantains (CARBAP, Njombe) and, after an acclimatization period of 1 month in the greenhouse, transferred to Mbouroukou.

In total, a plot of each cultivar was thus replicated nine times (nine plots per cultivar; 144 plants per cultivar). The three cultivars used for this experiment were: 'Banane Cochon' (*Musa* AAA, East African highland banana subgroup), 'Essong' (*Musa* AAB, plantain subgroup type French Giant) and 'Petite Naine' (*Musa* AAA, Cavendish subgroup); these cultivars are frequently cultivated by farmers in the Cameroon Highlands (Annex 2, Tézenas *et al.*, 1983; Swennen and Vuylsteke, 1987; Swennen, 1990). Henceforth in the text, these cultivars will sometimes be referred to as BC, FG and PN, respectively. The layout of the field is given in Figure 3.2.

Prior to uprooting the previous experiment, the roots and surrounding rhizosphere soil of the old *Musa* mats within each plot were sampled to determine the initial nematode population densities and to check whether random allocation of the replicates per cultivar had been successful (*i.e.* that initial nematode populations were similar for all cultivars within each block). One bulk sample of roots and one bulk sample of soil was collected per plot.

Prior to planting the new experiment, the old *Musa* mats from the previous experiment were uprooted. As some old *Musa* mats consisted of many generations of lateral shoots, an estimate of the quantity of nematode-infected root matter in the field was determined by counting the number of uprooted corms in each plot.

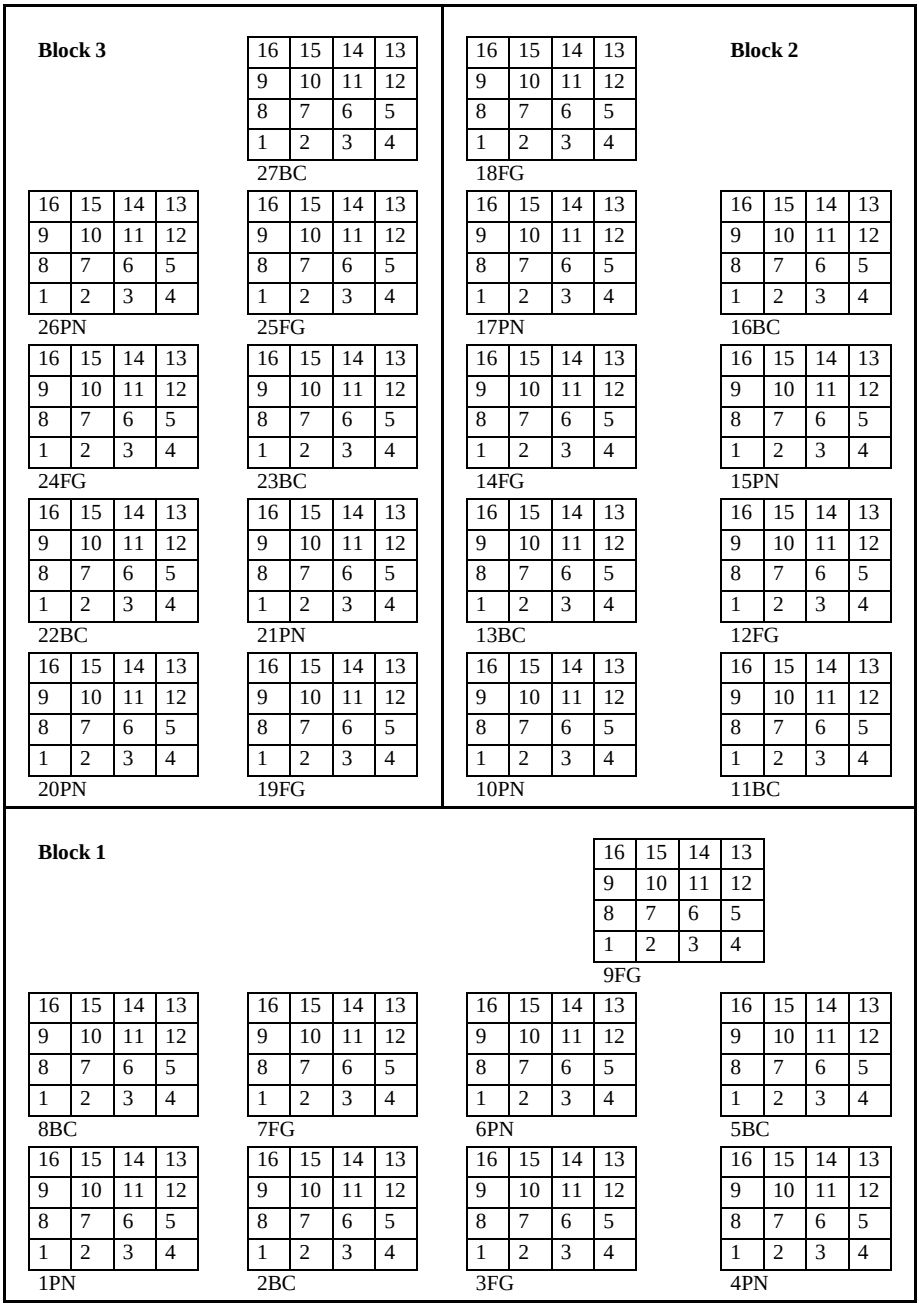

Figure 3.2: Map of the field experiment at the Mbouroukou research station (BC: Banane Cochon, FG: Essong, PN: Petite Naine; 1-16: plants within each plot).

Afterwards, the uprooted mats were chopped with a machete and left to rot in the field, allowing a gradual liberation of the nematodes into the soil surrounding the new plantlets. Planting was done in September 2003, one week after uprooting the previous *Musa* mats.

3.3.2 Field management

A systemic herbicide (active ingredient: glyphosate; trade name: Roundup ®) was applied before planting and every dry season thereafter. During the rainy season, weeds were manually slashed with a machete.

Weevil (*Cosmopolites sordidus*) trapping was done shortly after planting: pieces of pseudostem approximately 0.5 m long were cut lengthwise and placed in the field for a period of 1 week. Then, the number of weevils on these pseudostem pieces was assessed (Gold *et al.*, 1994). Dead leaves were removed with a machete when necessary. Desuckering was carried out once at 1 year after planting (YAP), whereby the mother plant and the largest following sucker were retained. As planting coincided with the end of the rainy season (2003), all plants were manually irrigated throughout their 1st dry season to ensure a higher rate of establishment. A low weevil infestation level was estimated, therefore one application of a broad-spectrum systemic insecticide (active ingredient: fipronil; trade name: Regent 5G) was applied at a rate of 30 g per plant around the base of each *in vitro* plantlet.

As the objective of this experiment was to estimate the potential damage caused by high nematode pressure, no nematicide was applied and plants were not propped as a management strategy. A photograph of the field experiment during the rainy season in 2004 is shown in Figure 3.3.

Figure 3.3: Mbouroukou field experiment in May 2004.

3.3.3 Data collection

3.3.3.1 Measurement of plant growth parameters

Monthly measurements

From 1 month after planting (MAP) until the end of the experiment (28 MAP), the following observations were made on each plant per plot:

- total number of leaves produced
- height of the mother plant (= vertical distance from the soil surface to the emergence point of the youngest unfurled leaf; cm)
- circumference at the soil surface (cm)

From desuckering (at 1 YAP) until the end of the experiment:

- number of suckers per plant.

Measurements at flowering

Plants were considered to have flowered when the inflorescence appeared. The assumption was made that one bract of the inflorescence opened per day. At flowering[1] the following observations were made:

- date of flowering = (Date of observation) – (number of fully opened bracts on the rachis)
- number of suckers
- length (L) and breadth (B) of the 3rd youngest leaf (m)
- number of standing leaves (NSL)
- total leaf area (TLA; Kumar *et al.*, 2002)[2]: TLA = L x B x 0,80 x NSL x 0,662 (m^2).

Measurements at harvest

Bunches were harvested when they were ripe according to local practice.
At harvest the following observations were made:

- date of harvest
- bunch weight (kg)
- fructification time span: (date of harvest) – (date of flowering).

Measurements at the end of the experiment (28MAP)

The experiment was ended at 830 days after planting (DAP).

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[1] Visits to the field experiment were made on a monthly basis, so some plant observations were made after the actual day of flowering.

[2] The total leaf area (TLA), as proposed by Kumar *et al.* (2002), has been criticized by Turner (2003) who proposed an alternate estimation method. The method proposed by Turner (2003) uses the length and breadth measurements of two leaves. For practical reasons we chose that of Kumar *et al.* (2002) as an approximation for the TLA. TLA presented in the results may, however, vary from the true TLA.

On plants that had not flowered the following observations were made:

- height of the mother plant (= vertical distance from the soil surface to the emergence point of the youngest unfurled leaf; cm)
- circumference at the soil surface (cm)
- number of suckers per plant
- total number of leaves produced
- length (L) and breadth (B) of the 3rd youngest leaf (m)
- number of standing leaves (NSL)
- total leaf area (TLA; Kumar *et al.*, 2002): TLA = L x B x 0,80 x NSL x 0,662 (m^2).

On plants that had flowered, but failed to produce a ripe bunch by 830 DAP the following observations were made:

- date of flowering.

On each *Musa* mat in the field (except those that failed to establish) the following observations were made:

- height of the mother plant and each sucker (except peeper suckers, cm)
- diameter at the soil surface of the mother plant and each sucker (except peeper suckers, cm).

Calculated indices

Using the observations measured during the field experiment, several additional indices were calculated to estimate:

- the vegetative growth per mat, not counting leaves or belowground plant parts, at the end of the experiment:
    - vegetative growth index (VGI, m^3): sum of the height of all plant parts per mat (incl. the height of the original mother plant) x (sum of the diameters of all plant parts per mat / 2)^2 x π.
- the rate of sucker growth and thus the development of the ratoon crop:
    - sucker growth index (SGI) (Ortiz and Vuylsteke, 1998; Tenkouano *et al.*, 2007): height of the following sucker divided by the height of the mother plant at flowering (for flowered plants) x 100.
- the robustness of plants and thus the likelihood to topple:
    - pseudostem index (Norgrove, 1999): (circumference / height) x 100.

3.3.3.2 Sampling of the Musa root system

The *Musa* root system is heterogeneous, due to the simultaneous occurrence within one mat of shoots belonging to different age classes. In order to keep the variability of nematode estimates to a minimum, samples were always taken from the mother plant, either at specific time intervals or at flowering, thus reducing variability due to environmental conditions or plant growth stage, respectively (Sarah, 1991).
Plants were sampled using the methodology described below. For samples taken prior to the set up of the experiment see section 3.3.1 Site, experimental design and field history.

Sampling at 1 YAP
Plants sampled at 1 YAP were chosen using the following procedure: an index of circumference x height was calculated for each plant. For each cultivar a box plot using this index was made (one graph for each block, data not shown). Plants that fell within 50% of all readings were labeled on a map of the field so that the plants used to estimate nematode population densities and root parameters at 1 YAP were not taller or smaller than 50% of all plants (within cultivar and block).
For each plant sampled, a 20 x 20 x 20 cm soil voilume was excavated adjacent to the corm of the mother plant. All roots found in this soil volume were collected and examined to determine the number of dead and functional roots. The number of dead and functional roots was estimated directly in the field. The root samples were then bulked per plot and the bulk sample was used to derive an estimate of the root necrosis index (RNI), the non-damaged root index (NDRI) and nematode population densities. In the laboratory, root samples were washed in tap water and 10 functional roots per plant were randomly chosen and sliced longitudinally. The root necrosis index (RNI) was visually estimated and calculated as follows: RNI = (necrotic cortical tissue/total cortical tissue) x 100% (Speijer and Gold, 1996; Speijer and De Waele, 1997). The RNI is an estimate of the root damage. The non-damaged root index (NDRI) was calculated as follows: NDRI = number of functional roots x (100-RNI) (Hauser, 2000). The NDRI is an estimate of the overall root system health. After scoring 10 roots from each sample to estimate the RNI, these roots were mixed with the other roots of the sample prior to extraction.

Sampling at flowering
Each plant that flowered was sampled as described above. Plants were sampled individually (*i.e.* no bulking was done); RNI and NDRI were estimated for each plant sampled.

Sampling at the end of the experiment
Roots of all remaining plants were sampled following the procedure used at flowering. Plants that had been sampled at 1 YAP but had not flowered by the end of the experiment were sampled a 2nd time at the end of the experiment. Plants that failed to establish were categorized as dead and were not sampled.

3.3.3.3 Extraction of nematodes from roots and soil

The methodology used to extract the nematode species from root samples, followed the procedures detailed in Chapter 2.
Nematode extraction from the rhizosphere soil was done by gravitation and decanting (Hooper, 1990). Soil sub-samples of 250 ml were mixed in a 10 litre bucket half-filled with tap water. After about 30 sec the suspensions were poured over a column of nested sieves of 50 and 32 µm apertures. The nematode suspensions remaining on the 50 and 32 µm aperture sieves were retained in a beaker and diluted to 100 ml with tap water.
After extraction, the soil samples were cleaned through centrifugal flotation (Hooper, 1990), as described in Chapter 2.

3.3.4 Yield: definitions, categories and yield loss analysis

Definitions of potential, attainable and actual yield adapted from Rabbinge (1993) *in* Casanova *et al.* (1999):

- potential yield: determined only by varietal characteristics and the seasonal pattern of environmental variables such as temperature and radiation. The potential yield is a theoretical yield achieved only under exceptional conditions, where no nutrients or environmental factors are growth-limiting;
- attainable yield: considerably lower than potential yield; observed under suboptimal amounts of water and nutrients;
- actual yield: lower than attainable yield; observed when growth-reducing factors, such as weeds, pests, diseases and pollutants are included in the model.

For our study we distinguished between the attainable yield and the actual yield which were calculated as follows:

- attainable yield: maximum bunch weight (kg) obtained per cultivar on this site x number of plants of that cultivar;
- actual yield: sum of all harvestable bunches per cultivar (kg).

When an estimate of production per plot was required, for example when analyzing the data using analysis of variance (ANOVA), the mean yield was used. Mean yield (kg) was calculated as follows:

- mean yield (per plot): percentage of harvested plants per plot x mean bunch weight of harvested plants per plot x 2500 plants (Mg/ha).

By the end of the experiment, all plants had been assigned to one of the following fate categories:

- pre-flowering: plants that failed to flower during the course of the experiment (from September 2003 – December 2005);
- toppled: plants that toppled pre- or post-flowering;
- flowered: plants that had produced a flower by the end of the experiment, but failed to reach harvest during the 28 months of the experiment;
- harvested: plants that produced an edible bunch before the end of the experiment;
- dead: plants that failed to establish and died (not due to toppling).

Yield loss was further partitioned in categories of plant loss following known effects of nematode infection on *Musa* productivity (Luc *et al.*, 2005):

1. failure to establish[1]: dead plants (not due to toppling)
2. lengthening of the growth cycle: pre-flowering and flowered but not harvested plants;
3. toppling: toppled pre- and post-flowering plants;
4. reduced bunch weight: within a cultivar, plants that produced a bunch with a weight lower than the maximum bunch weight for that cultivar.

For each cultivar, yield loss per category of plant loss was calculated as follows:

- for category of plant loss 1-3: yield loss (kg) = number of plants belonging to category (1-3) x maximum bunch weight;
- for category of plant loss 4: yield loss (kg) = (number of harvested plants x maximum bunch weight) – actual yield.

Finally, the relative yield loss (%) per plot was calculated for each category of plant loss as (yield loss / attainable yield) x 100, using the attainable yield for each cultivar and each field type, respectively. The relative yield loss per block was calculated using the mean maximum bunch weight of each cultivar.

3.3.5 Soil chemical properties

At 1 YAP, soil chemical properties per plot were assessed. A steel auger with a 20 mm core was used to sample soil at eight random places per plot. Samples were separated for depth classes 0-10, 10-20 and 20-30 cm in each of the plots. Samples were oven dried at 65 °C and ground to pass through a 0.5 mm sieve. pH was determined in a water suspension at a 2:5 soil/water ratio.

[1] Although not generally a direct effect of nematode infection, failure to establish was an important cause of yield loss in the current experiment, most likely linked to planting during the dry season.

Exchangeable Ca^{2+}, Mg^{2+}, K^{+} and available P were extracted using the Mehlich-3 procedure (Melich, 1984). Cations were determined by atomic absorption spectrophotometry and P by the malachite green colorimetric procedure (Motomizu *et al.*, 1983). Organic C was determined by chromic acid digestion and spectrophotometric procedure (Heanes, 1984). Total N was determined using the Kjeldahl method for digestion and ammonium electrode determination (Bremner and Mulvaney, 1982; Bremner and Tabatabai, 1972).

3.3.6 Accumulated weevil damage at 830 DAP

At the end of the experiment, each *Musa* mat (except those that failed to establish) was examined for weevil damage, as it became apparent that some plants had suffered weevil damage despite an apparently low weevil infestation level observed at the start of the experiment. Each mat was uprooted and the mother plant (or ratoon plant if the mother plant had been harvested) and each sucker (larger than the peeper sucker growth stage) were examined for weevil damage. Cross sections were made of each plant part at 5 cm below the collar by means of a machete. Assessments were carried out over a period of 2 weeks. Observed damage represented the accumulated damage caused by weevils over the course of the experiment.

Cross section damage to the cortex and central cylinder caused by the tunneling of the larvae of the banana weevil was estimated as follows: the absence or presence of weevil damage was evaluated in 16 sectors, using a grid drawn by the observer onto the exposed cross section of the corm (an adaptation of methods by Taylor, 1991, and Treverrow, 1994 *in* Messiaen, 2002). Damage was assessed separately for the cortex and the central cylinder in the belowground corm part of each plant part.

The cross-sectional damage (CSD) in the cortex (CoCSD) and cylinder (CyCSD) of each plant part, was calculated as follows:

- Co(Cy)CSD = number of sectors affected by weevil larvae (x) in the cortex (cylinder) divided by 16 sectors (x/16)

The average cross-sectional damage CSDav for the cortex (CoCSDav) and cylinder (CyCSDav) per mat were calculated as follows:

- Co(Cy)CSDav = sum of CoCSD (CyCSD) on the mother plant (or ratoon plant if the mother plant had been harvested) and each sucker (larger than the peeper sucker growth stage) divided by the number of plant parts per mat.

Total cross sectional damage (TCSD) was then calculated as follows:

- TCSD = CoCSDav + CyCSDav (with a maximum TCSD value of 32, if each sector of cortex and each sector of cylinder was affected).

The percentage of mats affected by weevil damage was calculated using the number of weevil-affected mats per plot, *i.e.* showing some form of damage in at least one plant part per mat.

3.3.7 Data handling and statistical procedures

The analysis of the results is divided into two sections:

- Results part I - Effect of field history and cultivar: describes the effect of field history and cultivar on plant growth and production.
- Results part II - Relationships between soil chemistry, nematode population densities, nematode-related root damage and production: describes the relationship between the variables observed during this study.

Calculation of growth rates

Regression analysis of plant growth parameters over time showed that plant growth was best approximated by a quadratic equation. However, the difference in R^2 of linear versus quadratic equations (with intercept = 0) was negligible (data not shown). Growth rates were therefore calculated assuming a linear growth.

Initial weekly growth rates (from 1-6 MAP) and mean weekly growth rates (from planting until flowering or until 830 DAP for non-flowering plants) were calculated using data per plant, except for plants that failed to establish or toppled.

Plant growth parameters measured at specific time intervals (1, 6, 12 MAP and at flowering) and the calculated growth rates were subjected to Analysis of variance (ANOVA) following the procedure detailed below.

Analysis of the effect of cultivar and field history

Differences between cultivars and field history were tested with two-way ANOVA. The full linear model is given in [1]

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha^* \beta)_{ij} + \varepsilon_{ijk} \qquad [1]$$

Whereby:

Y = bunch weight, mean yield, % harvested plants, days until flowering, root parameters, nematode population densities, growth parameters

μ = mean

α = effect of the factor Cultivar (i = Banane Cochon, Essong, Petite Naine)

β = effect of the factor Field History (j = Block I, Block II, Block III)

k = replicate 1, 2, 3

$(\alpha^* \beta)$ = effect of the interaction term

ε = residual error.

A Bonferroni correction was used when interactions were significant (p-value of the interaction x number of factors) to avoid the Type 1 error (= the error of rejecting a null-hypothesis when it is actually true), due to non-random distribution of the factor Field History. Differences with probabilities of $p<0.05$ are mentioned, using the probability classes $p<0.05$ and $p<0.01$. Post-hoc comparison of means were done using Tukey's HSD test (Kutner *et al.*, 2005).
When the interaction term was insignificant, the reduced model ANOVA was used:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \varepsilon_{ijk} \qquad [2]$$

For all ANOVA's, the homogeneity of variances was checked with the Levene's test whereby $p=0.015$ was used as a cut-off point, below which the error variances between groups were deemed heterogeneous. ANOVA is robust against deviations from homogeneity (Kutner *et al.*, 2005), when sample sizes are equal. Normality of the error terms was checked for each model using Q-Q plots and the Kolmogorov test for normality. ANOVA is also robust against deviations from normality (Lindman, 1974).
When either of the assumptions for ANOVA were grossly not met, a suitable transformation was applied: nematode population densities were ln (x+1) transformed and percentages (such as RNI) were square-root transformed (Gomez and Gomez, 1984). Untransformed means are presented in the tables for ease of comprehension, with a footnote if transformed means were used in the analysis. When transformation of a variable did not allow for ANOVA the Kruskal-Wallis (non-parametric ANOVA equivalent) test was used. This too is mentioned in a footnote to the tables where the results are presented.

Estimates of plot means
The number of plants that flowered per plot during this experiment was variable. Therefore, the means per plot of flowered plants were sometimes calculated from less than 16 observations. At 1 YAP, nematode population density estimates were made from one bulk sample of four plants per plot, while at other sampling times each plant was analyzed separately and the mean calculated per plot. For the means calculated from observations of pre-flowered plants at the end of the trial, plot data were sometimes missing (because each plant in some plots had flowered), resulting in an unbalanced two-way ANOVA for data from pre-flowering plants. Therefore, for ANOVA's using data obtained at 830 DAP only main effects were tested. The number of observations used to calculate the plot means throughout the experiment are presented in Table 3.2.

Table 3.2: Sample size used to calculate plot means at specified intervals and plant growth stages.

Cultivar	Field history	Replica	Plot	1 MAP G	6 MAP G	12 MAP G	12 MAP# N	FL G/N	HV G	PF G/N
PN	Block 1	1	1	16	16	16	4	16	15	0
BC	Block 1	1	2	16	16	14	4	6	3	8
FG	Block 1	1	3	16	16	15	4	11	8	3
PN	Block 1	2	4	16	16	16	4	15	14	1
BC	Block 1	2	5	16	16	14	4	13	10	1
PN	Block 1	3	6	16	16	16	4	16	10	0
FG	Block 1	2	7	16	16	13	4	2	1	8
BC	Block 1	3	8	16	16	16	4	10	7	3
FG	Block 1	3	9	16	16	13	4	7	2	5
PN	Block 2	1	10	16	16	16	4	11	8	4
BC	Block 2	1	11	16	16	16	4	14	12	2
FG	Block 2	1	12	16	16	15	4	10	8	1
BC	Block 2	2	13	16	15	14	4	5	2	2
FG	Block 2	2	14	16	15	13	4	2	2	8
PN	Block 2	2	15	16	16	16	4	16	16	0
BC	Block 2	3	16	16	16	15	4	13	13	0
PN	Block 2	3	17	16	16	11	4	16	15	0
FG	Block 2	3	18	16	16	16	4	14	10	1
FG	Block 3	1	19	16	16	16	4	15	11	1
PN	Block 3	1	20	16	16	16	4	16	16	0
PN	Block 3	2	21	16	16	16	4	16	16	0
BC	Block 3	1	22	16	16	16	4	14	14	1
BC	Block 3	2	23	16	15	15	4	14	14	0
FG	Block 3	2	24	16	16	16	4	12	8	4
FG	Block 3	3	25	16	16	16	4	10	8	6
PN	Block 3	3	26	16	16	16	4	15	15	1
BC	Block 3	3	27	16	16	15	4	16	16	0
Total n				432	429	407	27	325	274	60

G,N: growth, nematode parameters measured respectively; Each plot consisted of 16 plants, remaining plant fates are detailed in the results section; '#', bulk sampling of four plants per plot; MAP: months after planting; FL: flowered, HV: harvested, PF: still pre-flowered at the end of the experiment.

Analysis of the relative yield loss

In order to evaluate the contribution of each category of plant loss to the relative yield loss (%), two ANOVA procedures were carried out: (1) the data set

was split by category of plant loss (giving four data sets in total) and the relative yield loss was subjected to a reduced model ANOVA with block and cultivar as main effects; (2) the data set was split by field history and cultivar, respectively, (giving six data sets in total) and the relative yield loss was subjected to a one-way ANOVA with category of plant loss as a main effect.

Analysis of soil chemistry

The assessment of soil K^+ critical levels is subordinate to $K^+/Ca^{2+}/Mg^{2+}$ balance and several authors use the ratio $K^+/ K^++Ca^{2+}+Mg^{2+}$(Delvaux in Gowen 1995); therefore in the analysis of the soil data this ratio was used.

An ANOVA was used to determine whether significant differences were found in soil nutrient content per block and whether each cultivar was subjected to similar soil nutrient contents (procedure as described above, separate analysis for each depth class).

Analysis of the association between plant growth and production

Pearson correlations were used to analyze the level of association between plant growth and production. Prior to correlation analysis, the data were split by cultivar. Partial correlations, using days to flowering as a control variable[1], were used to examine the relationship between the total number of leaves produced and the bunch weight. All correlations were done using individual plant data.

Analysis of the relationship between nematode population densities, soil chemistry, root health and production

In the second part of the results section the relative importance of soil chemistry, nematode population densities and root damage for production is examined using standard multiple regression analysis. Figure 3.4 illustrates the relationships that were examined using multiple regression analysis. Analyses were carried out separately for each cultivar, using individual plant data. For the relationship depicted in Figure 3.4 by arrow (1), data of flowered plants were used; for arrows (2) and (3), data of harvested plants were used.

In multiple regression analysis, a model with extra predictors will tend to have a larger R^2. This is because each predictor will always "explain" some of the variation in the independent variable simply by chance. So, the more predictors that are added to the model, the more this effect will come into play. Adjusted R^2 is a conservative adjustment of R^2, using the following formula: Adjusted R^2

[1] A control variable is used to extract the variance it explains from each of the two initial correlated variables. The resulting partial correlation is the remaining correlation between the two initial variables once the variance explained by the control variable has been removed from each of them (Garson, 2010).

= 1- ((1- R^2)((1-n)/(1-n-k)), whereby n is the sample size and k is the number of independent variables.

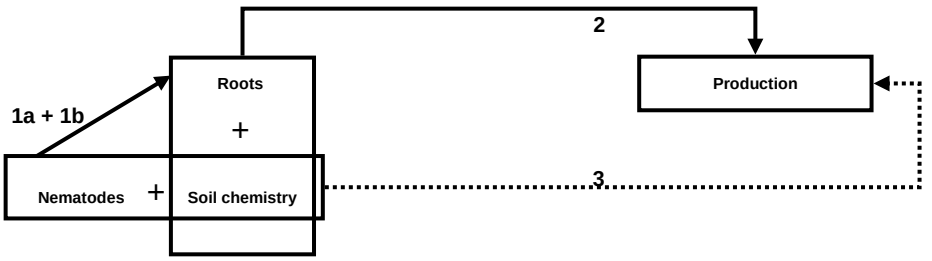

Figure 3.4: Relationships examined using standard multiple regression analysis:

(1) 1a: dependant variable RNI; predictor variables: *P. goodeyi*, *R. similis*, *Helicotylenchus* sp., *Meloidogyne* sp. and *Hoplolaimus* sp. (section 3.4.2.1); 1b: dependant variable: root parameter (number of dead/functional roots, RNI or NDRI); predictor variables: soil chemistry and *P. goodeyi* population densities (section 3.4.2.3)

(2) dependant variable: bunch weight; predictor variables: soil chemistry (soil Ca content), NDRI and number of dead roots (section 3.4.2.4)

(3) dependant variable: bunch weight; predictor variables: soil chemistry (soil Ca content) and *P. goodeyi* population densities (section 3.4.2.5)

In other words, adjusted R^2 is a downward adjustment of R^2 to adjust for one model having more degrees of freedom than another model (SPSS, 2006; Garson, 2009). The adjusted R^2 was therefore used to compare model performance, as it compensates for model complexity. The relative importance of each independant variable used in the models was evaluated by comparing their ß values, whereby higher ß values signify a relatively larger contribution. Beta (ß) values are the regression (b) coefficients for standardized data. As they are standardized values, they are independent of the unit in which they are measured. Beta (ß) is the average amount the dependent increases when the independent increases one standard deviation and other independent variables are held constant (Kutner *et al*., 2005; SPSS, 2006; Garson, 2009).

The appropriateness of the multiple regression models was evaluated by visual estimation of the normal probability plots of the residuals and plots of the standardized residuals against the standardized predicted values.

The model was deemed appropriate when the residuals approximated the normal distribution, variance of the error terms was constant and linearity of the relationship between the independent and dependent variables could be safely assumed. The following transformations were performed prior to analysis in order to improve the normality of the residuals: RNI was square root

transformed and *Pratylenchus goodeyi* population densities were ln (x+1) transformed.

The choice of independent variables is clarified in part II of the results section, as it follows from part I of the results section. When two independent variables were highly correlated ($r>0.90$), only one of the two variables was chosen in order to avoid multicollinearity. Multicollinearity refers to excessive correlation between independent variables, which leads to large standard errors of the b and beta coefficients, making it difficult or impossible to assess the relative importance of each variable.

All statistical analyses were done using SPSS for Windows, Student Version 14.0 (SPSS, Chicago, Illinois, USA) and SAS Enterprise Guide version 4.1 (SAS Institute Inc., Cary, NC, USA).

3.4 Results

3.4.1 Results part I - Effect of field history and cultivar

3.4.1.1 Defining the experiment site in terms of field history

Prior to planting, the highest ($p<0.05$) mean number of old corms from the previous experiment were found in the plots of Block 1 (on average 25 corms per plot). The mean number of old corms per plot in Block 2 was 13 (significantly less than in Block 1, $p<0.05$). No old corms were found in the plots of Block 3.

There was no difference in the number of old corms between plots assigned to the three cultivars to be used in the experiment and no interaction effect of block x plot assignment to cultivar was seen for the number of old corms ($p<0.05$; Table 3.3).

There was no significant difference in mean nematode population densities of individual nematode species found in the roots of previous *Musa* mats between Block 1 and Block 2. Over 90% of the nematodes found in the root samples of previous *Musa* mats from Block 1 and Block 2 were *P. goodeyi*, with *Meloidogyne* spp., *Helicotylenchus* spp. and *Hoplolaimus* spp. making up most of the remaining 10% (Table 3.3). *Radopholus similis* was found in only two plots (assigned to Banane Cochon and Petite Naine) in Block 2. More *Meloidogyne* spp. were found in the roots of previous *Musa* mats in plots assigned to Banane Cochon than in plots assigned to the other two cultivars ($p<0.05$), but nematode population densities were relatively low (0-800 *Meloidogyne* spp. per 100g FRW). No difference was seen in the soil nematode population densities per block or per plot assignment to cultivar.

Table 3.3: Labeling of field types in terms of nematode pressure using the mean (± standard error) root and soil nematode population densities extracted from the previous *Musa* mats and the mean (± standard error) number of old *Musa* corms prior to establishment of the field experiment.

Treatment		Roots of previous *Musa* mats						Rhizosphere soil		
Field history	No. of corms[#]	*P. goodeyi*	*Melo*	*Hoplo*	*Helico*	*R. similis*[θ]	*P.goodeyi* (%)	*P. goodeyi*	Total nematodes	*P. goodeyi* (%)
Block I (High nematode pressure)	25±3	22600±5656	385±97	59±34	67±25	0±0	97	4±1	36±9	15
Block II (Medium nematode pressure)	13±2	13808±3073	319±93	81±33	356±197	104±70	94	4±2	20±6	23
Block III (Low nematode pressure)	0±0	-	-	-	-	-	-	3±2	43±10	8
p-level	*	ns	ns	ns	ns	-		ns	ns	
Plot assignment to cultivar[§]										
Banane Cochon	13±4	17911±3358	622b ±66	78±50	344±254	89	93	1±1	18±4	5
Essong	12±3	21256±9712	156a ±56	78±44	89±33	0±0	96	4±2	41±9	18
Petite Naine	13±5	15445±1428	278a ±115	55±34	200±187	67	97	6±2	40±11	23
p-level	ns	ns	*	ns	ns	ns		ns	ns	

Melo: Meloidogyne spp.*; Hoplo: Hoplolaimus* spp.; *Helico: Helicotylenchus* spp.; [§]*: area of the field where the cultivars used in the current experiment were planted, after uprooting the previous Musa mats;* [#]*: number of corms of previous Musa mats;* '*': *significant difference between means at p<0.05;* 'ns': *not significant at p<0.05;* '-': *not applicable;* [θ]*: R. similis was found in only two plots; Nematode population densities represent the mean (n=9) number of nematodes per 100 g fresh root weight and mean number of nematodes per 100 ml for root and soil extractions, respectively; Means were separated using the Tukey's HSD test, means followed by the same letter are not significantly different at p<0.05.*

Given that the main objective of this study was to examine the effects of *P. goodeyi* infestation on the three *Musa* cultivars and that no difference was found between blocks in mean *P. goodeyi* population densities (both roots and soil; Table 3.3), nematode inoculum pressure could essentially be defined using the number of corms per plot, as each additional corm left to rot in the field increased the population densities of nematodes that could infect the *in vitro* plantlets. Therefore Block 1, Block 2 and Block 3 were labeled 'high nematode pressure', 'medium nematode pressure' and 'low nematode pressure', respectively. Henceforth referred to as field type HNP, MNP and LNP, respectively.

3.4.1.2 Effect of field history and cultivar on yield and yield loss

Table 3.4 shows the effect of field history and cultivar on the bunch weight of harvested plants (kg), percentage of harvested plants, yield (Mg/ha), number of days until flowering and fructification time span.

Table 3.4: Effect of field history and cultivar on the bunch weight of harvested plants (kg), percentage of harvested plants (%), yield (Mg/ha), number of days until flowering and fructification time span (± standard error).

Treatment	Bunch weight	Harvested plants	Yield	Days to flowering	Fructification time span
Field history	(kg)	(%)	(Mg/ha)		days
High nematode pressure (HNP)	14.7±1.6	48.6a±10.5	13.0a±2.9	612b±27	100a±7
Medium nematode pressure (MNP)	18.4±2.9	59.7ab±10.6	21.9ab±4.5	522a±31	116ab±4
Low nematode pressure (LNP)	17.6±1.5	81.9b±6.9	27.7b±2.0	521a±35	120b±3
p-level	ns	*	*	*	*
Cultivar					
Banane Cochon	13.1a±1.5	63.2ab±10.5	17.9±4.0	535a±31	107±3
Essong	23.1b±2.0	40.3a±7.8	19.3±4.5	639b±19	109±9
Petite Naine	14.4a±0.7	86.8b±6.0	25.5±2.6	481a±26	120±3
p-level	**	**	ns	**	ns

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment.*

No interaction effect of cultivar x field history was seen on bunch weight, percentage harvested plants, yield, days until flowering or fructification time span. Significant differences were seen among cultivars for bunch weight, percentage harvested plants and days until flowering ($p<0.01$). Significantly more plants were harvested for Petite Naine (86.8%) than for Essong (40.3%) ($p<0.05$). The heaviest mean bunch weight, however, was found for Essong (23.1 kg) compared to both Banane Cochon (13.2 kg) and Petite Naine (14.4 kg). The observed trend in the percentage of harvested plants on the one hand and mean bunch weights on the other hand, resulted in a similar mean yield for all cultivars ($p<0.05$).

Bunch weight was highest in the MNP field (18.4 kg), however, the difference with the bunch weights found in the HNP (14,7 kg) and LNP (17,6 kg) fields was not significant ($p<0.05$). The percentage harvested plants, yield and days until flowering were significantly affected by field history ($p<0.05$) with higher yields (27.7 Mg/ha) due to more harvested plants (81.9%) in the LNP field and lower yields (13 Mg/ha) due to less harvested plants (48.6%) in the HNP field.

The fructification time span in the HNP field was shorter than in the LNP field ($p<0.05$; see also correlations below). On average, Essong flowered almost 4 months later than Banane Cochon and Petite Naine ($p<0.05$) and plants in the HNP field flowered almost 3 months later than those in the LNP or MNP field ($p<0.05$). The observed difference in days until flowering between field types was due to differences in the cumulative rate of flowering (Figure 3.5). No difference was seen between cultivars in the fructification time span.

For harvested plants of each cultivar, plants that flowered earlier produced heavier bunches and were harvested earlier, despite longer fructification time spans than plants that flowered later (Table 3.5).

The heaviest bunches for each cultivar were not always found in the most productive field types. The heaviest bunch for Banane Cochon weighed 25 kg, two bunches of this weight were produced in the MNP field. The heaviest bunch for Essong weighed 45 kg, two bunches of this weight were produced in the MNP field. The heaviest bunches for Petite Naine weighed 26 kg, one bunch of this weight was produced in the HNP field and one in the LNP field.

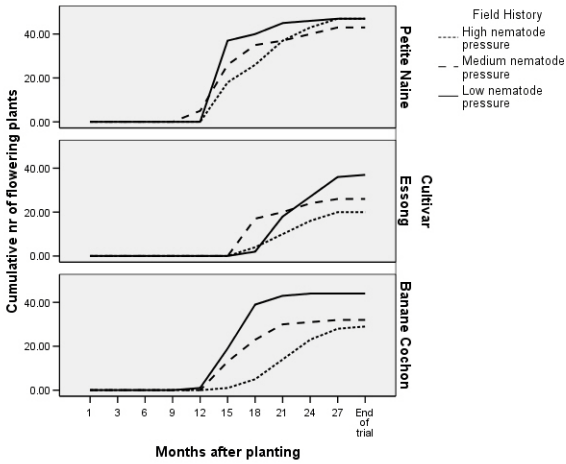

Figure 3.5: Cumulative number of flowering plants of Banane Cochon, Essong and Petite Naine from planting until the end of the experiment in three fields with varying nematode pressure.

Table 3.5: Pearson correlation coefficients and associated probabilities between days until flowering, fructification time span, days until harvest and bunch weight for harvested plants of the cultivars Banane Cochon, Essong and Petite Naine.

Cultivar		Days to flowering	Fructification time span (days)	Days to harvest	Bunch weight (kg)
Banane Cochon	Days to flowering	-	-0.382**	0.985**	-0.754**
	Fructification time span		-	-0.215*	0.501**
	Days to harvest			-	-0.702**
	Bunch weight				-
Essong	Days to flowering	-	-0.584**	0.955**	-0.664**
	Fructification time span		-	-0.315*	0.546**
	Days to harvest			-	-0.576**
	Bunch weight				-
Petite Naine	Days to flowering	-	-0.494**	0.985**	-0.578**
	Fructification time span		-	-0.335**	0.408**
	Days to harvest			-	-0.544**
	Bunch weight				-

***Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed); for BC n= 91, for FG n=58; for PN n=125*

Given that all plants originated from *in vitro* propagated plants, the assumption was made that each plant had an equal probability at the start of the experiment to produce a bunch as heavy as the heaviest bunch for that cultivar. This theoretically attainable yield for all cultivars combined would have been 13 824 kg in total. For Banane Cochon attainable yield would have amounted to 3600 kg (62.5 Mg/ha)1; for Essong 6480 kg (112.5 Mg/ha) and for Petite Naine 3744 kg (65 Mg/ha).

Not all plants produced such a heavy bunch however and the total actual yield was only 4512 kg for all cultivars or 33% of the attainable yield. For Banane Cochon actual yield was 1288 kg (17.8 Mg/ha; 28.5% of the attainable yield); for Essong 1388 kg (19.3 Mg/ha; 17.2% of the attainable yield) and for Petite Naine, 1836 kg (25.5 Mg/ha; 39.2% of the attainable yield).

Figure 3.6a gives an overview of the total number of plants per cultivar in each fate category at the end of the experiment according to field type. The temporal pattern of yield decline per cultivar and per field type is illustrated in Figure 3.6b. In each field type, 48 plants per cultivar were planted.

[1] Theoretically attainable yield = maximum bunch weight per cultivar x 144 plants per cultivar; [yield/ha = (theoretically attainable yield x 2500 plants/ha) / 144]; Mg = 1000 kg.

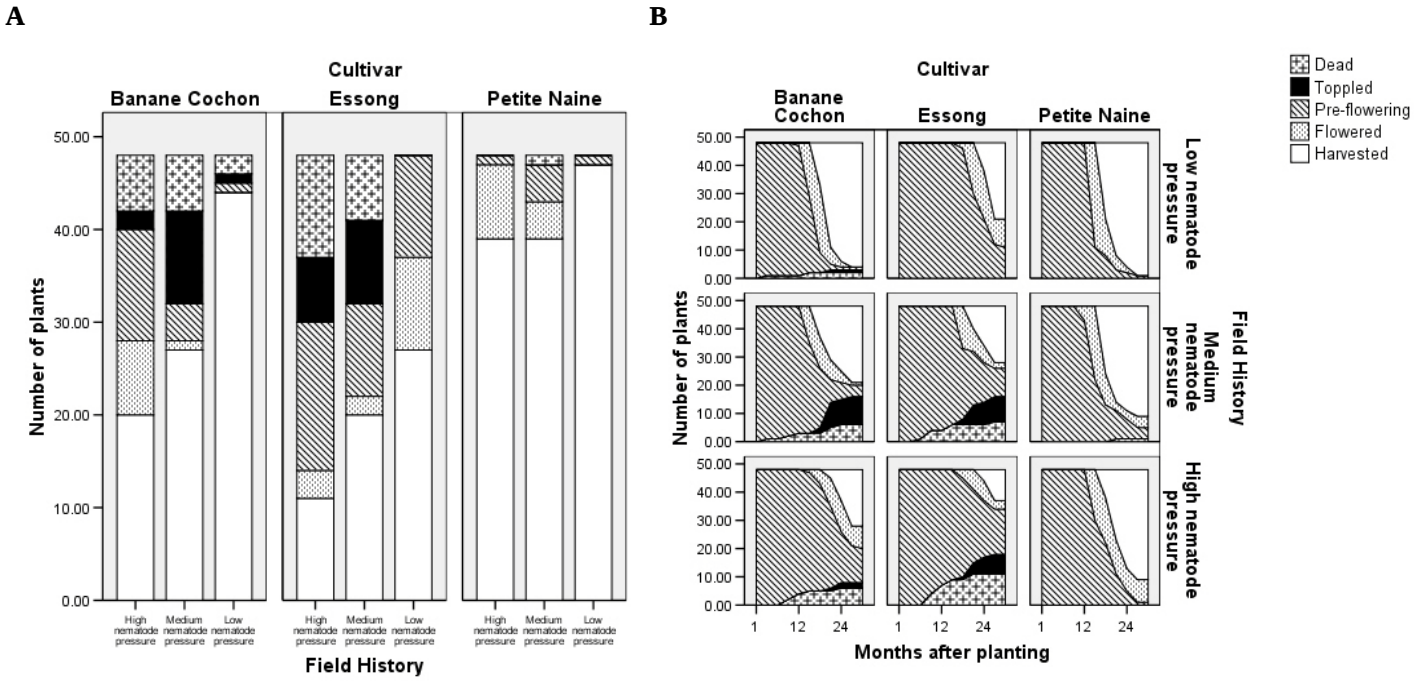

Figure 3.6: Effect of field history and differences among cultivars on (a) the number of plants per fate category at the end of the experiment and (b) the decline in yield potential from planting to the end of the experiment.

Figure 3.7 illustrates the total amount of yield loss (9312 kg) in each plant loss category relative to the attainable yield per cultivar within each field type. Of the 13824 kg attainable yield, 3623 kg was lost to reduced bunch weight, 3458 kg to lengthening of the growth cycle, 1186 kg to failure of plants to establish and 1045 kg to toppling, resulting in the above mentioned actual yield of only 4512 kg.

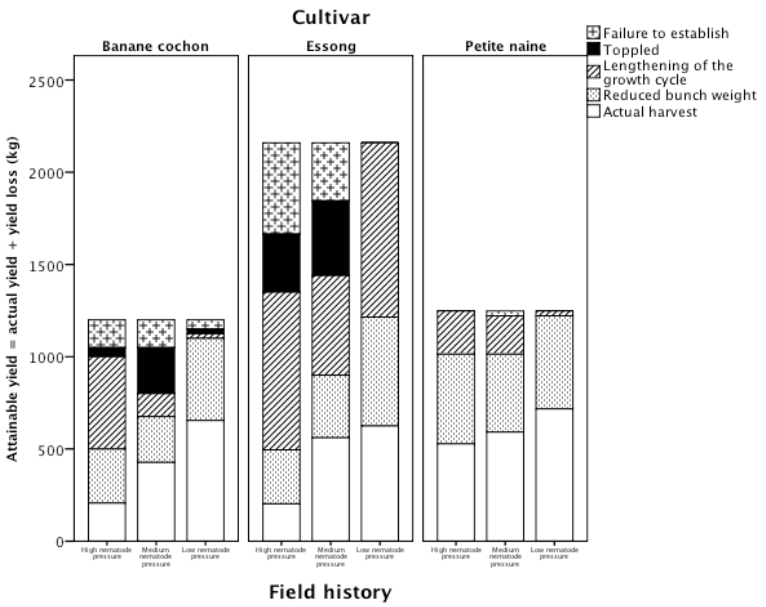

Figure 3.7: Effect of field history and differences among cultivars on the actual yield and on the nematode-related yield loss (kg).

The interaction effect of field history x cultivar on the percentage of plants within each category of plant loss was insignificant at $p<0.05$ (data not shown) allowing for a separate analysis of the effect of field history and cultivar on the relative yield loss. The results are presented in Table 3.6.

Effect of cultivar on the yield loss per category of plant loss

An effect of cultivar was seen on the relative yield loss within each category of plant loss ($p<0.01$). A higher relative yield loss due to failure to establish, lengthening of the plant growth cycle and toppling was seen for Essong compared to Petite Naine ($p<0.05$).

Table 3.6: Partitioning of the relative yield loss: structure of loss as affected by field history and cultivar.

	Attainable yield	Actual	Yield loss	Overall relative yield loss	Relative yield loss (%) per category of plant loss[#]				
Field history	kg	kg	kg	%[§]	FE	LG	RB	TO	p-within
High nematode pressure	4608	938	3670	79.6	14.0 ±6.0 AB	34.5 ±7.6 B	23.2 ±4.7 AB	7.9ab ±3.7 A	*
Medium nematode pressure	4608	1579	3029	65.7	10.7 ±5.1	18.9 ±7.5	21.9 ±3.7	14.2b ±5.5	ns
Low nematode pressure	4608	1996	2612	56.7	1.1 ±0.7 A	21.6 ±10.3 B	33.4 ±2.5 B	0.5a ±0.5 A	**
p-level					ns	ns	ns	*	
Cultivar									
Banane Cochon	3600	1288	2312	64.2	9.7ab ±3.1	18.1ab ±7.4	27.4ab ±4.6	9.0ab ±4.7	ns
Essong	6480	1388	5092	78.6	12.5b ±5.0 A	36.1b ±5.5 B	18.9a ±3.9 AB	11.1b ±3.7 A	**
Petite Naine	3744	1836	1908	51.0	0.7a ±0.7 A	12.5a ±5.5 B	37.8b ±2.3 C	0.0a ±0.0 A	**
p-level					*	*	**	*	

§: relative yield loss = (yield loss/attainable yield)x100; #: FE: failure to establish, LG: lengthening of the growth cycle, RB: reduced bunch weight, TO: toppling; Capital letters indicate a main effect of Category of plant loss within field type (or cultivar) at p<0.05; means followed by the same capital letter within a row are not different at p<0.05; Small letters indicate a main effect of field history (or cultivar) within a category of plant loss; means followed by the same small letter within a column are not significantly different at p<0.05; '': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; 'ns': no significant effect of treatment;; means± standard error of the mean.*

The highest relative yield loss due to reduced bunch weight was found for Petite Naine (37.8%) compared to Essong ($p<0.01$). The relative yield loss due to these categories of plant loss for Banane Cochon was intermediate between those found for Essong and Petite Naine.

Main cause of yield loss within each cultivar

Within the cultivars Essong and Petite Naine, differences were seen in the yield loss that could be attributed to each category of plant loss ($p<0.01$). For Essong, lengthening of the plant growth cycle (36.1%) was the most important cause of yield loss. For Petite Naine, reduced bunch weight (37.8%) was the single most

important cause of yield loss. For Banane Cochon, all categories of plant loss contributed equally to the yield loss.

Effect of field history on the yield loss per category of plant loss
An effect of field history was seen on the relative yield loss due to toppling, with higher losses registered in the MNP field (14.2%) compared to the LNP field (0.5%) ($p<0.05$). Other causes of yield loss were similar in the three field types. No significant difference (at $p<0.05$) was observed among field types for the losses due to failure to establish and lengthening of the plant growth cycle, although the relative yield loss due to these categories was generally lower in the LNP field compared to the HNP field. Losses due to reduced bunch weight were also similar among field types (not different at $p<0.05$), although a higher loss due to reduced bunch weight was seen in the LNP field compared to the other two field types.

Main cause of yield loss within each field type
Within the HNP field, the main cause of yield loss was lengthening of the plant growth cycle (34.5%) ($p<0.05$). Within the MNP field, no differences were seen in the causes of yield loss due to the four categories of plant loss. In the LNP field, the main cause of relative yield loss was due to reduced bunch weight (33.4%) and lengthening of the plant growth cycle (21.6%; $p<0.05$). Losses due to toppling and failure to establish in the LNP field were negligible (< 2%; $p<0.05$).

3.4.1.3 Relationship between plant growth and production

Slight differences were observed between cultivars in the strength of the relationship among plant growth and production parameters. The sign and significance of most correlations was the same however, with very few exceptions (Table 3.7).
Higher leaf emission rates and a larger total leaf area at flowering were associated with earlier flowering and larger bunch weights. Longer vegetative growth periods were associated with smaller bunch weights and more leaf production. Plants that were taller (except for Petite Naine) and had a larger circumference at flowering, flowered earlier and produced larger bunches. In summary, vigorous vegetative growth was associated with heavier bunches and earlier flowering.

Table 3.7: Pearson correlation coefficients and associated probabilities between vegetative growth and measurements at flowering for bunch producing plants of each cultivar.

Cultivar		Days to flowering	Bunch weight
Banane Cochon	No. of leaves	0.928**	-0.707**
	Leaf emission rate	-0.893**	0.721**
	Total leaf area	-0.546**	0.581**
	Height at flowering	-0.349**	0.398**
	Height at one year after planting	-0.919**	0.760**
	Mean weekly height increase	-0.922**	0.798**
	Circumference	-0.674**	0.616**
	Mean weekly circumference increase	-0.029	0.110
	No. of suckers	-0.502**	0.515**
	Pseudostem index	-0.265*	0.141
	Vegetative growth index	-0.285**	0.324**
			0.624**
Essong	No. of leaves	0.802**	-0.290*
	Leaf emission rate	-0.856**	0.770**
	Total leaf area	-0.656**	0.768**
	Height	-0.361**	0.516**
	Height at one year after planting	-0.880**	0.624**
	Mean weekly height increase	-0.847**	0.701**
	Circumference	-0.718**	0.798**
	Mean weekly circumference increase	0.058	0.155
	No. of suckers	-0.504**	0.652**
	Pseudostem index	-0.586**	0.510**
	Vegetative growth index	-0.032	0.084
Petite Naine	No. of leaves	0.788**	-0.338**
	Leaf emission rate	-0.831**	0.626**
	Total leaf area	-0.589**	0.569**
	Height	-0.149	0.359**
	Height at one year after planting	-0.902**	0.701**
	Mean weekly height increase	-0.875**	0.673**
	Circumference	-0.413**	0.669**
	Mean weekly circumference increase	-0.086	0.110
	No. of suckers	-0.490**	0.490**
	Pseudostem index	-0.342**	0.441**
	Vegetative growth index	-0.303**	0.372**

***Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed). For Banane Cochon n=91; for Essong n=58; for Petite Naine n=125.*

Table 3.8 gives the partial correlation coefficients between the number of leaves produced at flowering and the bunchweight while controlling for the effect of the date of flowering.

Table 3.8: Partial correlation coefficients and associated probabilities between the number of leaves at flowering and bunch weight, using days to flowering as a control variable.

Cultivar	Control variable		Bunch weight
Banane Cochon		No. of leaves	-0.031
Essong	Days to flowering	No. of leaves	0.541**
Petite Naine		No. of leaves	0.233*

***Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed). For Banane Cochon n=91; for Essong n=58; for Petite Naine n=125.*

When the days to flowering was used as a control variable, a positive relationship was observed between the bunch weight of the cultivars Essong and Petite Naine and the number of leaves produced at flowering; no relationship was observed between these variables for Banane Cochon. The rate of increase in plant height was more strongly associated with the number of days until flowering and bunch weight than was the height of plants at flowering. The rate of increase in circumference in contrast was not significantly associated with bunch weight. A higher correlation was observed between earlier pseudostem height measurements (at one year after planting) compared to the height at flowering. A higher number of suckers at flowering was associated with earlier flowering and larger bunches. Larger bunch weights were found for plants that had larger values for the pseudostem index and were thus less susceptible to topple as defined by their aboveground robustness (except for Banane Cochon). Mats that produced heavy bunches and flowered earlier, also had more vertical plant mass at the end of the experiment, indicated by the Vegetative Growth Index (VGI; except for Essong). Multiple regressions of bunch weight on height and circumference did not greatly improve the coefficients of multiple correlation obtained (data not shown).

3.4.1.4 Effect of field history and cultivar on the vegetative growth

The following tables (Tables 3.9-3.13) give an overview of the weekly plant growth rates, assuming linear growth, of vegetative growth parameters as affected by cultivar and/or field history. None of the vegetative growth parameters discussed in this section were affected by the interaction of cultivar x field history (at $p<0.05$).

Table 3.9 shows the effect of field history and cultivar on the number of leaves produced, weekly leaf emission rates and the total leaf area (TLA) at flowering.

Table 3.9: Effect of field history and cultivar on the number of leaves produced, weekly leaf emission rates (LER) and total leaf area (TLA) at flowering.

	No. of leaves produced				Weekly LER		TLA
Treatment	At 1 MAP	At 6 MAP	At 12 MAP	At Flowering[#]	1-6 MAP	Overall	m^2
Field history							
High nematode pressure	2.6 ±0.1	16.6 ±0.6	30.3a ±1.0	48.5 ±1.8	0.61 ±0.02	0.53a ±0.02	5.96 ±0.48
Medium nematode pressure	2.8 ±0.1	18.0 ±0.7	34.7b ±1.3	46.9 ±1.9	0.66 ±0.03	0.60b ±0.03	7.27 ±1.07
Low nematode pressure	2.7 ±0.1	17.3 ±0.5	35.9b ±0.7	46.9 ±2.1	0.64 ±0.02	0.62b ±0.02	7.34 ±0.63
p-level	ns	ns	**	ns	ns	**	ns
Cultivar							
Banane Cochon	3.0b ±0.1	16.9a ±0.4	32.3a ±1.1	45.2a ±1.3	0.60a ±0.02	0.58a ±0.02	6.51a ±0.56
Essong	2.4a ±0.1	16.0a ±0.6	33.0ab± 1.5	53.4b ±0.9	0.60a ±0.02	0.54a ±0.02	8.82b ±0.81
Petite Naine	2.7b ±0.1	19.1b ±0.4	35.6b ±0.9	43.7a ±1.3	0.72b ±0.02	0.64b ±0.02	5.24a ±0.34
p-level	**	**	*	**	**	**	**

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error of the mean; #: means of flowered plants; No.: number.*

At 1, 6 and 12 MAP, Petite Naine had produced the highest number of leaves since planting. Weekly leaf emission rates (LER) from 1-6 MAP and mean weekly LER were highest for Petite Naine, compared to Banane Cochon and Essong. The highest number of leaves at flowering was registered for Essong. This was however, due to the longer time until flowering (Table 3.7). From 1-6 MAP, field history had no effect on LER or on the total number of leaves produced. Overall though mean LER differed among field types, with lower LER in the HNP field. By 12 MAP, when all plants were still in the pre-flowering stage, this difference was measurable in the total number of leaves produced with a lower number of leaves in the HNP field. At flowering, field history had no effect on the total number of leaves produced. No effect was seen of field history on the total leaf area (TLA). Cultivar had a significant effect on the TLA, whereby Essong had a higher TLA compared to both Petite Naine and Banane Cochon ($p<0.01$).

Table 3.10 shows the effect of field history and cultivar on the height of plants at 1, 6 and 12 MAP, at flowering and on the mean weekly increase in height.

Table 3.10: Effect of field history and cultivar on the height of plants at 1, 6 and 12 MAP, at flowering and on the weekly increase in height.

	Height (cm)				Weekly increase (cm)	
Treatment	At 1 MAP	At 6 MAP	At 12 MAP	At flowering[#]	1-6 MAP	Overall
Field history						
High nematode pressure	21.6 ±1.3	46.5 ±3.4	105.2 ±12.1	256.5 ±30.2	1.09 ±0.10	2.46a ±0.23
Medium nematode pressure	19.6 ±0.6	57.7 ±6.8	169.2 ±27.2	288.0 ±38.1	1.66 ±0.28	3.33ab ±0.47
Low nematode pressure	18.9 ±1.0	46.3 ±3.7	169.3 ±13.3	282.2 ±32.2	1.19 ±0.15	3.58b ±0.28
p-level	ns	ns	ns	ns	ns	*
Cultivar						
Banane Cochon	19.9ab ±0.6	49.9 ±5.0	150.6 ±23.3	278.8b ±7.9	1.28 ±0.22	3.36 ±0.37
Essong	18.3a ±1.1	49.2 ±6.7	163.6 ±26.3	382.9c ±20.7	1.35 ±0.26	3.53 ±0.43
Petite Naine	21.8b ±1.1	51.5 ±3.4	129.4 ±10.0	165.0a ±3.3	1.30 ±0.13	2.47 ±0.21
p-level	*	ns	ns	**	ns	ns

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error of the mean; #: means of flowered plants.*

Weekly plant height increases from 1-6 MAP and mean plant height increases were both unaffected by cultivar. Although the first measurement at 1 MAP showed a plant height difference among cultivars, with Essong being the shortest cultivar, later measurements revealed no plant height differences among cultivars (Table 3.10). With the same steady increase in plant height for all three cultivars, the last cultivar to flower (Essong) was the tallest at flowering, followed by Banane Cochon. Petite Naine flowered earlier than the other cultivars and was the shortest cultivar at flowering. From 1-6 MAP, weekly plant height increase showed no differences among field types, overall though mean weekly plant height increase differed among field types ($p<0.05$), with the highest registered in the LNP field and the lowest in the HNP field. However, plant height measurements at 1, 6 and 12 MAP and at flowering were not significantly ($p<0.05$) affected by field history.

Table 3.11 shows the effect of field history and cultivar on plant circumferences at 1, 6 and 12 MAP, at flowering and on the mean weekly increase in circumference.

Table 3.11: Effect of field history and cultivar on the plant circumference at 1, 6 and 12 MAP, at flowering and on the weekly increase in plant circumference.

	Circumference (cm)				Weekly increase (cm)	
Treatment	At 1 MAP	At 6 MAP	At 12 MAP	At flowering[#]	1-6 MAP	Overall
Field history						
High nematode pressure	5.5b ±0.5	18.9 ±2.1	38.4a ±4.9	70.2 ±4.0	0.59 ±0.07	0.73a ±0.06
Medium nematode pressure	5.3ab ±0.3	22.5 ±2.6	57.0b ±6.7	80.6 ±4.9	0.75 ±0.11	0.99a ±0.11
Low nematode pressure	4.7a ±0.3	18.5 ±1.7	59.4b ±2.7	77.6 ±2.5	0.60 ±0.07	1.04b ±0.06
p-level	*	ns	*	ns	ns	*
Cultivar						
Banane Cochon	4.5a ±0.1	17.8a ±1.6	46.2 ±6.0	72.4a ±1.8	0.57a ±0.07	0.89 ±0.10
Essong	4.3a ±0.2	16.5a ±2.1	50.6 ±6.8	86.7b ±5.1	0.53a ±0.08	0.83 ±0.09
Petite Naine	6.6b ±0.3	25.7b ±1.5	57.9 ±4.2	69.4a ±1.7	0.83b ±0.07	1.04 ±0.08
p-level	**	**	ns	**	*	ns

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment;; means± standard error of the mean; [#]: means of flowered plants.*

An effect of cultivar was seen on the mean weekly increase in plant circumference from 1-6 MAP. Overall, however, the mean increase in plant circumference was similar for all cultivars. Initially, the plant circumference of Petite Naine increased more rapidly than that of Banane Cochon and Essong (Table 3.11). Consequently, Petite Naine had a larger circumference than the other two cultivars during this period. By 12 MAP, however, differences in plant circumference among cultivars were no longer apparent. At flowering, Essong had the largest plant circumference, mainly due to the longer period of vegetative growth of the mother plant. Field history had no effect on the weekly increase in plant circumference from 1-6 MAP, however, overall increase in plant circumference was highest in the LNP field and lowest in the HNP field. Initially, at 1 MAP, the plant circumference of plants in the LNP field was lowest but by 12 MAP it had grown to similar proportions as that found on plants in

the MNP field and the smallest plant circumference was of plants in the HNP field. On flowering plants no difference due to field history was measured in the plant circumferences.

The pseudostem index gives an indication of the susceptibility to topple, as shorter plants with a large plant circumference at ground level, will topple less easily than taller plants with a narrower circumference. Thus, the larger the pseudostem index the less susceptible a plant is, in theory, to topple pre- or post flowering. As a plant grows both plant height and circumference will increase, depending on the relative increase per parameter, the pseudostem index will be larger or smaller at successive sampling times. The effect of field history and cultivar on the pseudostem index at 1, 6 and 12 MAP, at flowering and on the change in pseudostem index from 1-6 MAP and from 6-12 MAP are given in Table 3.12.

Table 3.12: Effect of field history and cultivar on the pseudostem index at 1, 6 and 12 MAP and at flowering and on the change in pseudostem index from 1-6 MAP and from 6-12 MAP.

	Pseudostem index				Weekly change	
Treatment	At 1 MAP	At 6 MAP	At 12 MAP	At flowering[#]	1-6 MAP	6-12 MAP
Field history						
High nematode pressure	26.2 ±0.3	40.3 ±2.4	37.0 ±2.3	30.1 ±2.8	0.62 ±0.07	-0.12 ±0.03
Medium nematode pressure	27.9 ±1.5	40.5 ±3.2	35.9 ±2.5	30.9 ±3.1	0.55 ±0.08	-0.18 ±0.04
Low nematode pressure	25.6 ±1.2	40.2 ±2.4	36.0 ±2.1	30.3 ±3.1	0.64 ±0.07	-0.16 ±0.02
p-level	ns	ns	ns	ns	ns	ns
Cultivar						
Banane Cochon	23.6a ±0.7	36.4a ±0.5	31.9a ±0.8	26.1b ±0.3	0.56b ±0.04	-0.17ab ±0.03
Essong	25.0a ±0.9	33.9a ±0.5	31.8a ±0.7	23.0a ±0.3	0.39a ±0.04	-0.08b ±0.02
Petite Naine	31.0b ±0.9	50.7b ±1.0	45.2b ±0.5	42.2c ±0.4	0.86c ±0.03	-0.21a ±0.03
p-level	**	**	**	**	**	**

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment;; means± standard error of the mean; [#]: means of flowered plants.*

From 1-6 MAP, the pseudostem index increased for all plants. For the remaining vegetative growth phase (6-12 MAP), the pseudostem index gradually decreased for all plants. At each sampling time, the pseudostem index was highest for Petite Naine compared to the other cultivars. Increase in pseudostem index from 1-6 MAP was highest for Petite Naine followed by Banane Cochon and lowest for Essong. From 6-12 MAP, decrease was largest for Petite Naine and smallest for Essong. On flowered plants the lowest pseudostem index was found on Essong plants (high susceptibility to toppling) and highest on Petite Naine plants (low susceptibility to toppling).

The pseudostem index was not affected by field history at 1 and 6 MAP and rate of change in pseudostem index was similar in each field type. At 1 YAP, slight differences in growth rates of plant circumference and height (see above) resulted in lower pseudostem indices on plants in the HNP field compared to the other field types but this difference was no longer significant at flowering.

Table 3.13 shows the effect of field history and cultivar on the vertical vegetative growth per mat, as indicated by the number of suckers and the vegetative growth index, and on the sucker growth index.

At 1 YAP, the number of suckers produced by each mat was counted prior to desuckering. No difference was seen in the number of lateral shoots produced among cultivars at this time. On flowered plants, a cultivar-related difference in the number of suckers produced was seen with the highest number of suckers on Essong plants and the lowest number of suckers on Banane Cochon plants ($p<0.05$) (Table 3.13).Differences were seen among field types in the number of suckers produced at 1 YAP and at flowering ($p<0.05$). At both sampling times, the highest numbers of suckers were found on plants in the MNP field and the lowest number of suckers on plants in the HNP field. At the end of the experiment, however, when pre-flowering and flowered mats were jointly analyzed, no significant differences due to field history or cultivar were observed in the number of suckers per mat. The sucker growth index (SGI) is an indicator of the development of the ratoon crop.

Lower SGI values were observed for Essong. No effect was seen of field history on the SGI (Table 3.13). The vegetative growth index (m^3), an estimate of the volume of all aboveground plant parts per mat (except flower and leaves), was unaffected by cultivar or field history. Disregarding leaf production and bunch size, the aboveground vegetative growth was similar in the three field types and for each cultivar.

Table 3.13: Effect of field history and cultivar on vertical vegetative growth per mat as indicated by the number of suckers, the sucker growth index and the vegetative growth index.

Treatment	No. of suckers			Sucker growth index[§] (SGI)	Vegetative growth index (VGI; m³)
	At 12 MAP	At flowering[#]	At 830 DAP[§]	At 830 DAP	
Field history					
High nematode pressure	1.0a ±0.3	4.3a ±0.5	3.64 ±0.47	46.0 ±6.8	0.37 ±0.09
Medium nematode pressure	3.3b ±0.9	6.3b ±0.8	5.47 ±0.93	41.5 ±6.5	0.47 ±0.14
Low nematode pressure	2.6ab ±0.6	6.1ab ±0.5	5.50 ±0.40	45.2 ±8.8	0.74 ±0.28
p-level	*	*	ns	ns	ns
Cultivar					
Banane Cochon	2.0 ±0.6	4.8a ±0.4	4.38 ±0.56	61.6b ±5.5	0.79 ±0.28
Essong	1.7 ±0.9	6.8b ±0.8	5.29 ±0.48	19.3a ±2.6	0.23 ±0.04
Petite Naine	3.3 ±0.6	5.1ab ±0.5	4.93 ±0.48	51.8 ±2.7b	0.50 ±0.13
p-level	ns	*	ns	**	ns

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error of the mean; [#]: means of flowered plants; [§]: means of flowered and pre-flowering plants at the end of the experiment; No.: number.*

3.4.1.5 Effect of field history and cultivar on root parameters and nematode root population densities at fixed time intervals

Table 3.14 shows the effect of field history and cultivar on the root health and root damage parameters at 1 YAP. Field history and cultivar had no effect on the number of dead roots at 1 YAP. A significant effect of field history and cultivar was seen on the number of functional roots ($p<0.05$). More functional roots were found on the cultivar Petite Naine than on Essong and more functional roots were found on plants in the LNP field, compared to plants in the HNP field. No cultivar-related effect was observed on the RNI. RNI was significantly affected by field history ($p<0.01$).

Table 3.14: Effect of field history and cultivar on root parameters of pre-flowered plants of three *Musa* cultivars at 1 YAP.

Treatment				
Field history	No. of Dead roots	No. of Functional roots	RNI (%)	NDRI
High nematode pressure	0.75 ±0.22	15.36a ±1.32	27.6b ±3.4	1135a ±134
Medium nematode pressure	0.86 ±0.26	19.58ab ±1.34	15.3a ±2.8	1675ab ±154
Low nematode pressure	0.40 ±0.15	22.26b ±2.71	6.7a ±3.1	2122b ±264
p-level	ns	*	**	**
Cultivar				
Banane Cochon	0.72 ±0.25	19.56ab ±1.60	13.1 ±3.2	1733ab ±198
Essong	0.40 ±0.08	15.20a ±2.07	22.2 ±4.3	1224a ±179
Petite Naine	0.89 ±0.26	22.44b ±1.94	14.3 ±4.7	1975b ±254
p-level	ns	*	ns	*

RNI: root necrosis index; NDRI: non-damaged root index; '': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error of the mean; No.: number.*

Plants in the HNP field had the highest RNI compared to plants from the other field types. NDRI was significantly affected by field history and cultivar ($p<0.05$), with higher NDRI for Petite Naine compared to Essong and a higher NDRI on plants in the LNP field compared to plants in the HNP field.

Table 3.15 shows the effect of field history on the nematode root population densities at 1 YAP and compares the observed nematode population densities among cultivars. No differences were seen in the nematode root population densities among cultivars at 1 YAP. Higher *P. goodeyi* population densities were recovered from the roots of plants in the HNP and MNP field compared to the LNP field ($p<0.01$). As *P. goodeyi* was the most abundant nematode species found, this was reflected in the total nematode population densities ($p<0.01$). *Hoplolaimus* spp. and *R. similis* population densities were highest in the MNP field ($p<0.01$). There was no significant effect of field history on the *Meloidogyne* spp. and *Helicotylenchus* spp. root population densities at 1 YAP.

Table 3.15: Effect of field history on nematode root population densities of pre-flowered plants for three *Musa* cultivars at 1 YAP.

	Nematode population densities at 1YAP (individuals per 100g fresh root weight)					
Treatment						
Field history	Pg	Melo	He	Ho	Rs	TOT
High nematode pressure	32059b ±4905	1778 ±470	1229 ±259	207a ±95	0a ±0	35273b ±4849
Medium nematode pressure	25905b ±4130	1541 ±292	978 ±275	1112b ±267	2014b ±986	31550b ±4318
Low nematode pressure	1452a ±541	1971 ±785	577 ±415	504ab ±111	0a ±0	4518a ±1177
p-level	**	ns	ns	**	**	**
Cultivar						
Banane Cochon	17120 ±5981	1912 ±632	711 ±185	414 ±147	415 ±296	20572 ±5792
Essong	19156 ±4987	1438 ±303	1422 ±454	785 ±302	607 ±464	23423 ±5257
Petite Naine	23140 ±6629	1941 ±650	651 ±237	623 ±193	992 ±992	27347 ±7061
p-level	ns	ns	ns	ns	ns	ns

Pg: Pratylenchus goodeyi; Melo: Meloidogyne spp.*; He: Helicotylenchus* spp.; *Ho: Hoplolaimus* spp.; *Rs: Radopholus similis; TOT: total nematode population densities; '*': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; R. similis population densities analyzed using Kruskal-Wallis test; means± standard error of the mean.*

Table 3.16 shows the effect of field history and cultivar on the root health and root damage parameters at flowering. At flowering, more dead roots were found in the MNP field than in the HNP and LNP fields ($p<0.05$). The highest number of functional roots was found on plants in the LNP field and the lowest number in the HNP field. The root necrosis index was lower on plants in the LNP field compared to plants of the other two field types and, consequently, the NDRI, which is a function of both the number of functional roots and the RNI was highest in the LNP field. Cultivar had a significant effect on all root parameters measured at flowering, with the lowest number of dead roots and functional roots on plants of Essong.

The highest RNI and lowest NDRI at flowering was observed on Essong in comparison to the other cultivars used in this experiment ($p<0.01$). The interaction effect of cultivar x field history was not significant (at $p<0.05$) for all root parameters measured at flowering.

Table 3.16: Effect of field history and cultivar on root parameters of three *Musa* cultivars at flowering.

Treatment	No. of dead roots	No. of functional roots	RNI (%)	NDRI
Field history				
High nematode pressure	2.0a ±0.3	12.7a ±0.5	43.4b ±3.0	740a ±58
Medium nematode pressure	3.1b ±0.6	13.7ab ±1.6	37.6b ±5.4	922a ±180
Low nematode pressure	1.0a ±0.2	18.0b ±1.9	14.8a ±2.3	1559b ±182
p-level	*	*	**	**
Cultivar				
Banane Cochon	2.8b ±0.6	15.6ab ±2.0	28.3a ±5.3	1199b ±217
Essong	1.1a ±0.2	11.5a ±0.5	43.1b ±5.5	667a ±79
Petite Naine	2.1ab ±0.4	17.2b ±1.5	24.4a ±4.2	1354b ±171
p-level	**	*	**	**

RNI: root necrosis index; NDRI: non-damaged root index; '': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error; No.: number.*

Table 3.17 shows the effect of field history and cultivar on the nematode root population densities at flowering and the percentage *P. goodeyi* of the total nematode population densities. The highest total nematode population densities were found in the roots of plants in the HNP field, followed by plants in the MNP field. The lowest total nematode root population densities were found on plants in the LNP field ($p<0.01$). Between 76% (LNP) and 95% (HNP) of the total nematode population densities extracted from the roots at flowering were *P. goodeyi*.

The differences observed in the total nematode population densities were thus mainly due to differences in the population densities of this nematode. *Helicotylenchus* spp. and *R. similis* population densities were also higher in the HNP and MNP field compared to the LNP field. *Meloidogyne* spp. population densities by contrast were highest in the LNP field compared to the other field types. Cultivar had a significant effect on the root population densities of *P. goodeyi* and by consequence on the total nematode population densities. Other species population densities extracted from the roots at flowering did not differ between cultivars (at $p<0.01$).

Table 3.17: Effect of field history on nematode population densities in the roots of three *Musa* cultivars at flowering.

	Nematode population densities at flowering (individuals per 100g fresh root weight)						
Treatment	Pg	Melo	He	Ho	Rs	TOT	% Pg
Field history							
High nematode pressure	87980c ±3459	2467a ±367	663b ±78	276 ±74	796ab ±570	92194c ±8277	95.4
Medium nematode pressure	51055b ±10752	2422a ±405	580b ±98	525 ±161	5882b ±2199	60471b ±10294	84.4
Low nematode pressure	18875a ±6841	5473b ±1326	216a ±45	200 ±48	40a ±29	24815a ±7091	76.1
p-level	**	*	**	ns	*	**	
Cultivar							
Banane Cochon	39831a ±11618	3366 ±996	441 ±91	198 ±53	4015 ±2280	47856a ±10602	83.2
Essong	69279b ±14328	4294 ±1247	547 ±113	366 ±160	1296 ±786	75781b ±13726	91.4
Petite Naine	48800ab ±11769	2703 ±337	471 ±101	438 ±93	1406 ±1130	53843ab ±12409	90.6
p-level	*	ns	ns	ns	ns	*	

Pg: Pratylenchus goodeyi; Melo: Meloidogyne spp.*; He: Helicotylenchus* spp.; *Ho: Hoplolaimus* spp.; *Rs: Radopholus similis; TOT: total nematode population densities; '*': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; R.similis population densities were ln-transformed prior to analysis; means± standard error.*

The highest *P. goodeyi* (and total) population densities were found in the roots of Essong (69279 *P. goodeyi* per 100 g FRW) and the lowest population densities were found on the cultivar Banane Cochon (39831 *P. goodeyi* per 100 g FRW) ($p<0.05$). Population densities of *P. goodeyi* extracted from the roots of Petite Naine at flowering were intermediate between those found on Essong and Banane Cochon. The interaction effect of cultivar x field history was not significant ($p<0.05$) for all nematode population densities measured at flowering. Final sampling was undertaken at the end of the experiment over a period of 2 weeks, during the dry season of 2005. Plants that were still in the pre-flowering stage were sampled to estimate root health and nematode population densities.

Table 3.18 shows the effect of field history and cultivar on the root health parameters of pre-flowering plants at 830 DAP. No difference was seen in the number of functional or dead roots observed on plants depending on field history.

Table 3.18: Effect of field history and cultivar on root parameters of pre-flowering plants of three *Musa* cultivars at the end of the experiment (830 DAP).

Treatment		No. of dead roots	No. of functional roots	RNI (%)	NDRI
Field history	N				
High nematode pressure	7	1.9 ±0.5	15.5 ±1.6	26.4ab ±3.2	1115b ±97
Medium nematode pressure	6	1.8 ±0.6	12.0 ±2.0	39.9b 8.2	695a ±147
Low nematode pressure	5	0.8 ±0.4	14.1 ±0.6	14.7a 2.6	1205b ±76
p-level		ns	ns	*	**
Cultivar					
Banane Cochon	6	2.1 ±0.5	15.9 ±1.4	23.5 ±4.7	1180 ±74
Essong	9	1.6 ±0.4	13.5 ±1.4	32.1 ±6.7	921 ±133
Petite Naine	3	0.6 ±0.6	11.3 ±2.0	22.8 ±5.0	876 ±218
p-level		ns	ns	ns	ns

RNI: root necrosis index; NDRI: non-damaged root index; '': means are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error; No.: number.*

The highest RNI was found on pre-flowering plants in the MNP field (39.9%) followed by plants in the HNP field (26.4%; $p<0.01$). The lowest RNI was found on pre-flowering plants in the LNP field (14.7%).A significant effect was seen of field history on the NDRI, with highest NDRI on plants in the LNP field (1205) and lowest NDRI on plants in the MNP field (695) ($p<0.01$). Differences in the mean number of dead and functional roots, the RNI and NDRI did not differ among cultivars (at $p<0.05$).

Table 3.19 shows the effect of field history and cultivar on nematode population densities of pre-flowering plants at 830 DAP. A significant effect of field history was seen on the total nematode population densities extracted from the roots of pre-flowering plants at 830 DAP ($p<0.05$) with highest nematode population densities in the roots of pre-flowering plants in the MNP (33395 nematodes per 100g FRW) and HNP field (30062 nematodes per 100g FRW) and lowest nematode population densities in the roots of pre-flowering plants in the LNP field (9997 nematodes per 100g FRW) ($p<0.05$).

Table 3.19: Effect of field history and cultivar on nematode population densities of pre-flowering plants of three *Musa* cultivars at the end of the experiment (830 DAP).

		Nematode population densities at 830 DAP (individuals per 100g fresh root weight)						
Treatment		Pg	Melo	He	Ho	Rs	TOT	%Pg
Field history	N							
High nematode pressure	7	24957 ±3947	2045 ±1186	246 ±117	2 ±2	2812 ±2034	30062ab ±3677	83.02
Medium nematode pressure	6	25417 ±7070	647 ±172	139 ±58	78 ±44	7113 ±3266	33395b ±7807	76.11
Low nematode pressure	5	7951 ±4366	1414 ±471	126 ±54	26 ±26	480 ±480	9997a ±4415	79.53
p-level		ns	ns	ns	ns	ns	*	
Cultivar								
Banane Cochon	6	23534 ±5966	1880 ±1416	253 ±145	0 ±0	1717 ±1544	27385 ±5178	85.94
Essong	9	21442 ±5299	1002 ±288	133 ±34	46 ±31	3641 ±2123	26264 ±6569	81.64
Petite Naine	3	10924 ±5469	1656 ±508	155 ±59	66 ±38	7230 ±5300	20032 ±8945	54.53
p-level		ns	ns	ns	ns	ns	ns	

Pg: Pratylenchus goodeyi; Melo: Meloidogyne spp.*; He: Helicotylenchus* spp.; *Ho: Hoplolaimus* spp.; *Rs: Radopholus similis; TOT: total nematode population densities; '*': means are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error.*

Individual species population densities found in the roots of pre-flowering plants at 830 DAP were not significantly affected by field history nor cultivar (at $p<0.05$). Total root nematode population densities of pre-flowering plants were also not affected by cultivar.

3.4.1.6 Effect of field history on nematode population build up and composition

In general, nematode population densities accumulated over time with the highest population densities extracted from flowering plants (Figure 3.8a). Pre-flowering plants evaluated at 1 YAP and at the end of the experiment consistently had fewer root nematodes. Over time, the nematode community structure changed most in the roots of *Musa* mats planted in the LNP field. At 1 YAP, less than half of the nematodes extracted from plants in the LNP field were *P. goodeyi*.

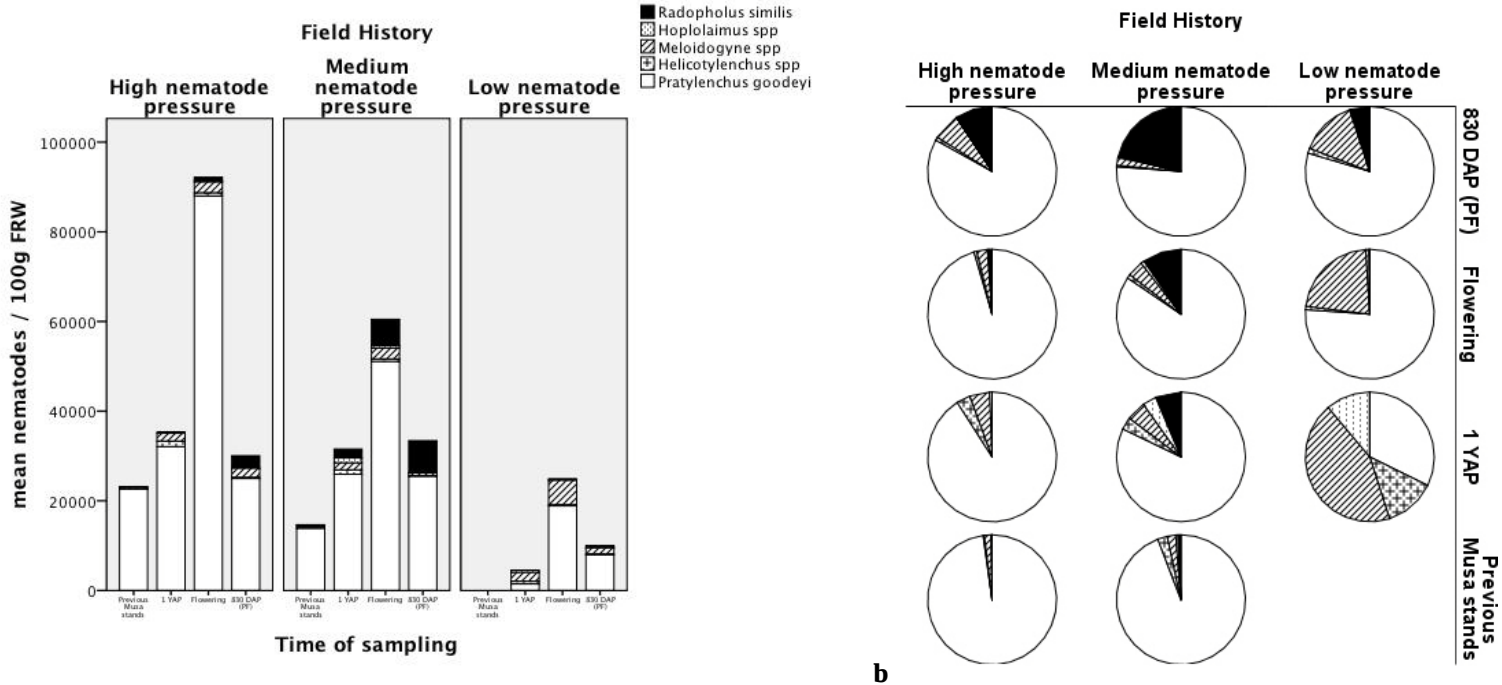

Figure 3.8: Nematode population build up (a) and composition (b) at consecutive sampling times: prior to experiment establishment on previous *Musa* mats, at 1 YAP, at flowering and on pre-flowered plants at the end of the experiment (830 days after planting).

At flowering, however, more than 75% of all nematodes extracted were *P. goodeyi*. In the HNP and MNP fields, nematode community structure resembled those extracted from the previous *Musa* mats, with a strong predominance of *P. goodeyi* over the other nematode species (Figure 3.8b). The proportion of *R. similis* in the roots of plants from both the HNP and MNP fields steadily grew from 1 YAP until flowering and the proportion of *R. similis* on pre-flowered plants at the end of the experiment was higher than that found on flowered plants. However, root population densities of *P. goodeyi* predominated the nematode community structure in all fields (Figure 3.8b).

3.4.1.7 Effect of field history and cultivar on weevil damage observations at 830 DAP

Weevil damage parameters per mat, at the end of the experiment are presented in Table 3.20.

Table 3.20: Effect of field history and cultivar on the total cross-sectional damage (TCSD) and the percentage of attacked plants by the end of the experiment.

Treatment		
Field history	TCSD	Attacked plants (%)
High nematode pressure	4.23 ±1.43	63.19ab ±9.85
Medium nematode pressure	4.77 ±1.56	70.83b ±8.40
Low nematode pressure	3.95 ±1.70	56.94a ±10.44
p-level	ns	*
Cultivar		
Banane Cochon	2.99a ±0.79	72.92b ±5.21
Essong	9.57b ±1.09	88.89c ±2.02
Petite Naine	0.38a ±0.12	29.17a ±4.29
p-level	**	**

'': means (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error of the mean.*

There was no interaction effect of field history x cultivar on the accumulated total cross sectional damage per mat (TCSD = sum of the average cortex- and

cylinder cross sectional damage) at the end of the experiment. Field history had no effect on TCSD (at $p<0.05$). A significant difference in TCSD was seen between cultivars, however, with the highest TCSD on Essong plants compared to the other two cultivars ($p<0.01$; Table 3.20). The mean TCSD for Essong was 9.6, for Banane Cochon 3.0 and for Petite Naine 0.4.In total 64% of all plants in this experiment showed some form of weevil damage by the end of the experiment on at least one plant part (the mother plant, the ratoon or lateral shoots) per mat.

There was no interaction effect of field history x cultivar on the percentage of mats attacked (at $p<0.05$). An effect of field history and of cultivar was seen on the percentage of mats attacked by weevils. The highest percentages were found on Essong (88.9%), followed by Banane Cochon (72.9%) and Petite Naine (29.2%). A higher percentage of plants were attacked by weevils in the MNP field (70.8%) compared to the LNP field (56.9%). Sixty-three percent of all plants in the HNP field showed some form of weevil damage.

3.4.2 Results part II: Relationship between soil chemistry, nematode population densities, root damage and production

3.4.2.1 Relationship between root necrosis and nematode population densities

The descriptive statistics and correlation coefficients of the nematode population densities with the root necrosis index per cultivar are given in Table 3.21. For each cultivar, the strongest association with root necrosis was observed with population densities of *P. goodeyi* ($p<0.01$). For Banane Cochon, *R. similis* densities were also significantly correlated with RNI ($p<0.05$) and for Petite Naine, *Meloidogyne* spp. and *Helicotylenchus* spp. were also significantly correlated with RNI ($p<0.05$). *Hoplolaimus* spp. was not significantly associated with RNI on any of the cultivars used in this experiment (Table 3.21).

The results of the standard multiple regression analysis of the RNI on the population densities of *P. goodeyi*, *Meloidogyne* spp., *Helicotylenchus* spp., *Hoplolaimus* spp. and *R. similis* are given in Table 3.22.

species for the RNI observed at flowering, on each cultivar (for Banane Cochon, ß[1] = 0.59; for Essong, ß = 0.72; for Petite Naine ß = 0.64; $p<0.01$; Table 3.22).

[1] beta values are the regression (b) coefficients for standardized data, and thus independent of the unit of measurement (see also section 3.3.7).

Table 3.21: Correlations between (square root-transformed) root necrosis index (RNI) of Banane Cochon, Essong and Petite Naine at flowering and (ln-transformed) nematode population densities.

Cultivar		Mean ± st.dev	RNI	*P. goodeyi*	*Meloido-gyne* spp.	*Helico-tylenchus* spp.	*Hoplolaimus* spp.	*R. similis*
Banane	RNI	4.46 ± 2.21	-	0.600**	0.081	0.109	-0.028	0.220*
Cochon	*P. goodeyi*	8.23 ± 3.69		-	0.140	0.119	0.056	0.084
n=105	*Meloidogyne* spp.	6.22 ± 3.26			-	0.114	0.129	0.031
	Helicotylenchus spp.	2.92 ± 3.23				-	0.124	0.108
	Hoplolaimus spp.	1.91 ± 2.88					-	0.084
	R. Similis	1.60 ± 3.48						-
Essong	RNI	5.99 ± 2.22	-	0.700**	-0.154	0.039	-0.049	0.056
n=83	*P. goodeyi*	9.59 ± 2.63		-	-0.176	0.143	0.107	0.067
	Meloidogyne spp.	7.08 ± 2.70			-	0.050	-0.033	0.093
	Helicotylenchus spp.	3.01 ± 3.34				-	.119	0.100
	Hoplolaimus spp.	2.13 ± 3.07					-	-0.117
	R. Similis	1.06 ± 2.70						-
Petite	RNI	4.36 ± 2.29	-	0.630**	0.148*	0.148*	-0.099	0.062
Naine	*P. goodeyi*	8.26 ± 3.98			0.170*	0.177*	0.078	0.196*
n=137	*Meloidogyne* spp.	7.00 ± 2.05				0.069	-0.011	0.160*
	Helicotylenchus spp.	3.72 ± 3.10					0.163*	0.036
	Hoplolaimus spp.	2.95 ± 3.24						0.116
	R. Similis	0.86 ± 2.60						

*Data of flowered plants; *:p<0.05; **:p<0.01; RNI: square root transformed root necrosis index (%); The ln-transformed root population densities of* P. goodeyi, Meloidogyne *spp.,* Helicotylenchus *spp.,* Hoplolaimus *spp. and* Radopholus similis are expressed */100g fresh root weight; Std. dev.: standard deviation.*

The standard multiple regression equations gave significant models for each cultivar, using nematode species population densities to predict RNI. Of all nematodes extracted from the roots, *P. goodeyi* was the single best predictive Other nematode species that contributed significantly to the model, added very little extra explanatory value to the models. Respectively 37%, 48% and 40% of the variation observed in the RNI could be explained for Banane Cochon (Adjusted $R^2 = 0.37$, $p<0.01$), Essong (Adjusted $R^2 = 0.48$, $p<0.01$) and Petite Naine (Adjusted $R^2 = 0.40$, $p<0.01$) using the nematode population densities found in the roots at flowering.

Table 3.22: Regression of (square root-transformed) RNI of three *Musa* cultivars at flowering and (ln-transformed) nematode population densities.

Cultivar		b	ß
Banane	Intercept	1.45**	
Cochon	*P. goodeyi*	0.35**	0.59**
	Meloidogyne spp.	0.00	0.00
	Helicotylenchus spp.	0.02	0.03
	Hoplolaimus spp.	-0.06	-0.08
	Radopholus similis	0.11*	0.17*
	R^2	0.40	
	Adj. R^2	0.37	
	Std. Error of the Estimate	1.76	
	p-value	**	
Essong	Intercept	0.67	
	P. goodeyi	0.60**	0.72**
	Meloidogyne spp.	-0.02	-0.03
	Helicotylenchus spp.	-0.03	-0.05
	Hoplolaimus spp.	-0.09	-0.12
	Radopholus similis	0.00	0.00
	R^2	0.51	
	Adj. R^2	0.48	
	Std. Error of the Estimate	1.61	
	p-value	**	
Petite	Intercept	1.20	
Naine	*P. goodeyi*	0.37**	0.64**
	Meloidogyne spp.	0.05	0.04
	Helicotylenchus spp.	0.04	0.06
	Hoplolaimus spp.	-0.11*	-0.15*
	Radopholus similis	-0.05	-0.05
	R^2	0.43	
	Adj. R^2	0.40	
	Std. Error of the Estimate	1.77	
	p-value	**	

*Data of flowered plants; *:p<0.05; **:p<0.01; The ln-transformed root population densities of* P. goodeyi, Meloidogyne *spp.*, Helicotylenchus *spp.*, Hoplolaimus *spp. and* Radopholus similis are expressed */100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.2 Effect of field history and cultivar on soil chemical properties

Correlations between soil chemistry variables are presented in Table 3.23. The mean soil chemical properties in the depth classes 0-10 cm, 10-20 cm and 20-30 cm in each of the three field types are presented in Table 3.24. An effect of field history was seen on soil chemical properties in almost all depth classes and for all soil variables examined (Table 3.24). No effect of cultivar was observed on the soil chemical properties at 1 YAP, indicating that the three cultivars were subject to similar (not different at $p<0.05$) soil chemistry.

Table 3.23: Correlations between soil chemistry variables (average of 0-10 cm, 10-20 cm and 20-30 cm per plot, n=27).

	pH	N	C	C/N	Ca^{2+}	Mg^{2+}	K^{+}	P
pH	-	0.723**	0.712**	0.427*	0.810**	0.790**	0.695**	0.660**
N		-	0.958**	0.535**	0.851**	0.811**	0.443*	0.774**
C			-	0.751**	0.781**	0.724**	0.396*	0.662**
CN				-	0.338	0.265	0.167	0.169
Ca^{2+}					-	0.980**	0.736**	0.915**
Mg^{2+}						-	0.698**	0.939**
K^{+}							-	0.565**
P								-

***Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed).*

Two patterns in the difference between field types could be discerned. Firstly, for soil N, organic C content, C/N ratio and the $K^{+}/K^{+}+Ca^{2+}+Mg^{2+}$ ratio: no difference was seen in the nutrient content of plots located in the MNP and LNP fields and the values were consistently higher (except $K^{+}/K^{+}+Ca^{2+}+Mg^{2}$) than those found in the HNP field ($p<0.01$). This pattern persisted at all depths, with only a few exceptions: no difference was observed among field types in the soil N content in the depth class 0-10 cm and the C/N ratio in the depth class 20-30 cm.

A second pattern could be discerned for the soil cation content in all depth classes and soil pH in the 0-10 cm depth class: no difference was seen in the nutrient content of plots located in the HNP and LNP fields and the values were consistently lower than those found in the MNP field ($p<0.01$). As the soil content of K^{+}, Ca^{2+} and Mg^{2+} are reflected in the $K^{+}/K^{+}+Ca^{2+}+Mg^{2}$ ratio, and this ratio is not different in the MNP and LNP fields; the second pattern remains for the soil P content (Table 3.24). Soil pH followed pattern one in the 20-30 cm depth class and pattern two in the 0-10 cm depth class. No difference was seen between field types for soil pH in the 10-20 cm depth class. All soil chemistry variables (disregarding depth classes) were strongly intercorrelated (Table 3.23).

Table 3.24: Soil chemical properties in the depth classes 0-10, 10-20 and 20-30 cm in fields with high-, medium- and low-nematode pressure at one year after planting.

Depth	Field History	pH H_2O	Total N%	Total C%	C/N ratio	Ca^{2+} cmol/kg	Mg^{2+} cmol/kg	K^+ cmol/kg	P ppm	$K^+/(K^+{+}Ca^{2+}{+}Mg^{2+})^{\#}$
0-10 cm	HNP	5.14a ±0.07	0.36 ±0.02	4.33a ±0.24	12.13a ±0.49	1.43a ±0.21	1.03a ±0.14	1.68a ±0.18	4.68a ±0.33	0.42b ±0.02
	MNP	5.58b ±0.06	0.39 ±0.01	5.38b ±0.17	13.73b ±0.27	3.93b ±0.54	2.60b ±0.46	2.65b ±0.16	10.80b ±1.92	0.31a ±0.03
	LNP	5.31a ±0.05	0.38 ±0.01	5.42b ±0.13	14.10b ±0.12	2.44a ±0.34	1.71ab ±0.24	1.59a ±0.13	7.60ab ±1.23	0.29a ±0.02
	p-value	**	ns	**	**	**	**	**	*	**
10-20 cm	HNP	5.02 ±0.08	0.27a ±0.00	3.68a ±0.11	13.81a ±0.29	0.80a ±0.15	0.62a ±0.12	1.27a ±0.16	3.35a ±0.20	0.49b ±0.03
	MNP	5.23 ±0.11	0.35b ±0.02	5.31b ±0.20	15.39b ±0.26	3.56b ±0.61	2.38 ±0.51b	2.10b ±0.18	9.05b ±1.90	0.29a ±0.03
	LNP	5.25 ±0.05	0.33b ±0.01	5.11b ±0.11	15.35b ±0.25	1.77a ±0.31	1.09a ±0.15	1.19a ±0.11	4.45a ±0.70	0.31a ±0.02
	p-value	ns	**	**	**	**	**	**	**	**
20-30 cm	HNP	4.60a ±0.08	0.22a ±0.01	3.09a ±0.12	14.27 ±0.32	0.60a ±0.16	0.42a ±0.12	1.04ab ±0.13	2.21a ±0.14	0.55b ±0.03
	MNP	5.05b ±0.10	0.33b ±0.02	4.94b ±0.30	15.14 ±0.45	2.49b ±0.48	1.65b ±0.39	1.38b ±0.14	5.88b ±1.36	0.29a ±0.03
	LNP	5.13b ±0.07	0.33b ±0.01	4.87b ±0.12	14.94 ±0.16	1.35ab ±0.27	0.79ab ±0.14	0.87a ±0.09	3.19ab ±0.56	0.31a ±0.02
	p-value	**	**	**	ns	**	**	**	*	**

'': means± standard error of the mean (n=9) are significantly different at p<0.05; '**': significantly different at p<0.01; means followed by the same letter in a column are not different at p<0.05; 'ns': no significant effect of treatment; means± standard error of the mean; '#': The assessment of soil K critical levels is subordinate to $K^+/Ca^{2+}/Mg^{2+}$ balance and several authors use $K^+/(K^+{+}Ca^{2+}{+}Mg^{2+})$ ratio (Delvaux* in *Gowen 1995).*

In the following multiple regression models, the relationship between nematode population densities, soil chemical properties and production is discussed. In order to avoid artificially inflating R^2 values through the addition of redundant variables, a selection of independent variables was made as follows:

1. For nematode population densities: only (ln-transformed) *P. goodeyi* was used in the standard multiple regression models as it was the main cause of root necrosis and higher population densities of *P. goodeyi* were found in comparison to other nematode species.
2. For root health: the number of dead roots and the non-damaged root index (NDRI) were used as explanatory variables in the multiple regression. The number of functional roots and the root necrosis index (RNI) were not used as the NDRI is a function of both variables.
3. For soil chemical properties: data of plants were divided using the observed pattern in soil chemical properties between field types (Table 3.24). Using the similarities between the low nematode pressure (LNP) and medium nematode pressure (MNP) fields, plants in these two fields were grouped to form a first data set; a second data set comprised of plants planted in the high nematode pressure (HNP) field. In this way, all soil chemistry variables (or their associated index, as for K, Mg and Ca) were similar (not different at $p<0.05$) for plant data in this first data set (from the MNP and LNP fields). However, soil P content still differed ($p<0.05$) between the MNP and LNP fields (cf. Table 3.24). Therefore, soil P content was included in the models to allow for variations in this variable.

Thus, for the regression analyses (Figure 3.4), the following datasets were used:

- data set-1: HNP plants: lower soil chemistry values;
- data set-2: MNP and LNP plants: higher soil chemistry values.

Most of the soil chemistry variables measured in this experiment are macro-nutrients important for *Musa* growth. For all soil parameters, higher values are generally better. Data set-1 and data set-2 therefore represent relatively less and more fertile soils, respectively.

No difference was seen between field types in the observed weevil damage per plant. Weevil damage was therefore not included in these models.

A summary of the results of sections 3.4.2.3, 3.4.2.4 and 3.4.2.5 is given at the end of the results section (Table 3.49a, 3.49b and 3.49c).

3.4.2.3 Effect of soil P content and *Pratylenchus goodeyi* population densities on the number of dead and functional roots, root necrosis index and the non-damaged root index

3.4.2.3.1 Dead roots regressed on *Pratylenchus goodeyi* population densities and soil P content in more fertile soils

The descriptive statistics and correlations of the number of dead roots with soil P content and (ln-transformed) *P. goodeyi* population densities in more fertile soils are given in Table 3.25.

Table 3.25: Correlations between the number of dead roots of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively more fertile soils of the experimental site

			Correlation coefficients		
Cultivar		Mean±std. deviation	Dead roots	P	*P. goodeyi*
Banane cochon	Dead roots	2.62 ± 2.85	-	0.221*	0.085
n=76	P	7.43 ± 3.35		-	-0.238*
	P. goodeyi	7.33 ± 3.75			-
Essong	Dead roots	0.97 ± 1.31	-	0.316*	0.508**
n=63	P	8.11 ± 6.77		-	0.468**
	P. goodeyi	9.30 ± 2.52			-
Petite Naine	Dead roots	2.03 ± 2.51	-	0.062	0.246**
n=90	P	5.93 ± 2.19		-	0.502**
	P. goodeyi	6.81 ± 4.20			-

*Data of flowered plants used; * p<0.05; ** p<0.01; dead roots: number of dead roots; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; std. deviation: standard deviation.*

Soil P content was positively correlated with the number of dead roots for Banane Cochon and Essong but not with the number of dead roots of Petite Naine. *Pratylenchus goodeyi* population densities in roots of Essong and Petite Naine were positively correlated with the number of dead roots at flowering; but not with the number of dead roots on Banane Cochon. The results of the standard multiple regression analysis of the number of dead roots on *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.26.

Table 3.26: Regression of the number of dead roots at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* population densities at flowering and soil P content in relatively more fertile soil.

Cultivar		b	ß
Banane	Intercept	0.19	
Cochon	P	0.22*	0.26*
	P. goodeyi	0.11	0.15
	R^2	0.07	
	Adj. R^2	0.04	
	Std. Error of the Estimate	2.80	
	p-value	ns	
Essong	Intercept	-1.42*	
	P	0.02	0.10
	P. goodeyi	0.24**	0.46**
	R^2	0.27	
	Adj. R^2	0.24	
	Std. Error of the Estimate	1.14	
	p-value	**	
Petite	Intercept	1.42	
Naine	P	-0.09	-0.08
	P. goodeyi	0.17*	0.29*
	R^2	0.07	
	Adj. R^2	0.04	
	Std. Error of the Estimate	2.46	
	p-value	*	

*Data of flowered plants used; * p<0.05; ** p<0.01; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

The results of the multiple regression analysis show that, although the models were significant for Petite Naine and Banane Cochon, very little of the variation seen in the number of dead roots on plants in more fertile soils could be explained using root population densities and soil P content (Adjusted $R^2<0.10$; $p<0.01$). For Essong, 24% of the variation in the number of dead roots could be explained with this model (Adjusted $R^2 = 0.24$, $p<0.01$), whereby *P. goodeyi* root population densities at flowering was the better unique predictor variable

(ß = 0.46, p<0.01). Soil P content did not contribute significantly to the model for Essong.

3.4.2.3.2 Dead roots regressed on *Pratylenchus goodeyi* population densities and soil P content in less fertile soils

The descriptive statistics and correlation statistics of the number of dead roots with soil P content and (ln-transformed) *P. goodeyi* population densities in less fertile soils are given in Table 3.27.

Table 3.27 Correlations between the number of dead roots of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively less fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Dead roots	P	*P. goodeyi*
Banane cochon	Dead roots	2.38 ± 3.31	-	-0.262	0.147
n=29	P	3.13 ± 0.58		-	0.302
	P. goodeyi	10.61 ± 2.21			-
Essong	Dead roots	1.23 ± 1.68	-	-0.078	0.104
n=20	P	3.65 ± 0.17		-	0.249
	P. goodeyi	10.51 ± 2.83			-
Petite Naine	Dead roots	2.28 ± 3.29	-	0.083	0.089
n=47	P	3.45 ± 0.58		-	0.076
	P. goodeyi	11.04 ± 0.85			-

*Data of flowered plants used; * p<0.05; ** p<0.01; dead roots: number of dead roots; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; std. deviation: standard deviation.*

No significant correlations were observed between the predictor and dependent variables. The results of the standard multiple regression analysis of the number of dead roots on *P. goodeyi* population densities and soil P content in relatively less fertile soils are given in Table 3.28. These models show that *P. goodeyi* population densities at flowering and soil P content were unable to explain any of the variation observed in the number of dead roots in less fertile soils. This was the case for each cultivar.

Table 3.28: Regression of the number of dead roots at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* population densities at flowering and soil P content in relatively less fertile soil.

Cultivar		b	ß
Banane	Intercept	4.42	
Cochon	P	-1.91	-0.34
	P. goodeyi	0.37	0.25
	R^2	0.12	
	Adjusted R^2	0.06	
	Std. Error of the Estimate	3.21	
	p-value	ns	
Essong	Intercept	4.34	
	P	-1.07	-0.11
	P. goodeyi	0.08	0.11
	R^2	0.02	
	Adjusted R^2	-0.01	
	Std. Error of the Estimate	1.76	
	p-value	ns	
Petite	Intercept	-2.73	
Naine	P	0.43	0.08
	P. goodeyi	0.32	0.08
	R^2	0.01	
	Adjusted R^2	-0.03	
	Std. Error of the Estimate	3.35	
	p-value	ns	

*Data of flowered plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3.3 Functional roots regressed on *Pratylenchus goodeyi* population densities and soil P content in more fertile soils

The descriptive statistics and correlations of the number of functional roots with soil P content and (ln-transformed) *P. goodeyi* population densities in more fertile soils are given in Table 3.29.

Table 3.29: Correlations between the number of functional roots of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively more fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Functional roots	P	*P. goodeyi*
Banane Cochon	Functional roots	18.74 ± 9.10	-	0.370**	-0.548**
n=76	P	7.43 ± 3.35		-	-0.238*
	P. goodeyi	7.33 ± 3.75			-
Essong	Functional roots	11.43 ± 4.13	-	0.024	-0.290*
n=63	P	8.11 ± 6.77		-	0.468**
	P. goodeyi	9.30 ± 2.52			-
Petite Naine	Functional roots	19.32 ± 8.95	-	-0.039	-0.386**
n=90	P	5.93 ± 2.19		-	0.502**
	P. goodeyi	6.81 ± 4.20			-

*Data of flowered plants used; * p<0.05; ** p<0.01; functional roots: number of functional roots; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; std. deviation: standard deviation.*

The number of functional roots observed at flowering was negatively correlated with the population densities of *P. goodeyi* on all three cultivars ($p<0.05$). Soil P content was positively correlated with the number of functional roots on Banane Cochon. The results of the standard multiple regression analysis of the number of functional roots on *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.30. For all three cultivars, the multiple regression model was significant, however, the amount of variation in the number of functional roots at flowering that could be explained using these models, varied depending on the cultivar. For Banane Cochon, more than 30% of the variation in the number of functional roots could be explained using soil P content and *P. goodeyi* root population densities (Adjusted R^2 = 0.34, $p<0.01$), whereas for the other two cultivars, less variation was explained using these two variables (for Essong Adjusted R^2 = 0.09, $p<0.05$; for Petite Naine Adjusted R^2 = 0.16, $p<0.01$; Table 3.30). In all three models, *P. goodeyi*

root population densities was the better unique predictor variable (for Banane Cochon ß = -0.49; for Essong ß = -0.39; for Petite Naine ß = -0.49). Soil P content did not contribute significantly to the models for Essong and Petite Naine.

Table 3.30: Regression of the number of functional roots at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* population densities at flowering and soil P content in relatively more fertile soil.

		b	ß
Banane	Intercept	22.28**	
Cochon	P	0.69*	0.25*
	P. goodeyi	-1.18**	-0.49**
	R^2	0.36	
	Adjusted R^2	0.34	
	Std. Error of the Estimate	7.38	
	p-value	**	
Essong	Intercept	16.31**	
	P	0.13	0.20
	P. goodeyi	-0.63**	-0.39**
	R^2	0.12	
	Adjusted R^2	0.09	
	Std. Error of the Estimate	3.95	
	p-value	*	
Petite	Intercept	21.44**	
Naine	P	0.84	0.21
	P. goodeyi	-1.04**	-0.49**
	R^2	0.18	
	Adjusted R^2	0.16	
	Std. Error of the Estimate	8.20	
	p-value	**	

*Data of flowered plants used; * p<0.05; ** p<0.01; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3.4 Functional roots regressed on *Pratylenchus goodeyi* population densities and soil P content in less fertile soils

The descriptive statistics and correlations of the number of functional roots with soil P content and (ln-transformed) *P. goodeyi* population densities in less fertile soils are given in Table 3.31. *Pratylenchus goodeyi* root population densities were negatively correlated with the number of functional roots of Banane Cochon.

Table 3.31: Correlations between the number of functional roots of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively less fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Functional roots	P	*P. goodeyi*
Banane cochon	Functional roots	11.66 ± 4.48	-	-0.017	-0.371*
n=29	P	3.13 ± 0.58		-	0.302
	P. goodeyi	10.61 ± 2.21			-
Essong	Functional roots	12.16 ± 4.74	-	-0.260	-0.125
n=20	P	3.65 ± 0.17		-	0.249
	P. goodeyi	10.51 ± 2.83			-
Petite Naine	Functional roots	13.98 ± 5.99	-	-0.256	0.038
n=47	P	3.45 ± 0.58		-	0.076
	P. goodeyi	11.04 ± 0.85			-

*Data of flowered plants used; * p<0.05; ** p<0.01; functional roots: number of functional roots; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; std. deviation: standard deviation.*

No significant correlations were observed among *P. goodeyi* population densities and the number of functional roots of Petite Naine and Essong in less fertile soils. In relatively less fertile soils, soil P content was not significantly correlated with the number of functional roots for any of the cultivars. The results of the standard multiple regression analysis of the number of functional roots on *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.32. The multiple regression models using soil P content and *P. goodeyi* population densities were unable to explain any of the variation observed in the number of functional roots observed at flowering on Banane Cochon, Essong or Petite Naine in less fertile soils (Table 3.32).

Table 3.32: Regression of the number of functional roots at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* population densities at flowering and soil P content in relatively less fertile soil.

Cultivar		b	ß
Banane	Intercept	22.44**	
Cochon	P	-1.23	-0.15
	P. goodeyi	-0.64	-0.32
	R^2	0.16	
	Adj. R^2	0.10	
	Std. Error of the Estimate	4.26	
	p-value	ns	
Essong	Intercept	37.46	
	P	-6.61	-0.24
	P. goodeyi	-0.11	-0.07
	R^2	0.07	
	Adj. R^2	-0.04	
	Std. Error of the Estimate	4.83	
	p-value	ns	
Petite	Intercept	11.59	
Naine	P	-0.20	-0.02
	P. goodeyi	0.28	0.04
	R^2	0.002	
	Adj. R^2	-0.04	
	Std. Error of the Estimate	6.12	
	p-value	ns	

*Data of flowered plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3.5 Root necrosis index regressed on *Pratylenchus goodeyi* population densities and soil P content in more fertile soils

The descriptive statistics and correlations of the root necrosis index (RNI) with soil P content and (ln-transformed) *P. goodeyi* population densities in more fertile soils are given in Table 3.33.

Table 3.33: Correlations between the (square root transformed) root necrosis index (RNI) of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively more fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	RNI	P	*P. goodeyi*
Banane Cochon	RNI	3.85 ± 2.02	-	-0.145	0.554**
n=76	P	7.43 ± 3.35		-	-0.238*
	P. goodeyi	7.33 ± 3.75			-
Essong	RNI	5.63 ± 2.20	-	0.419**	0.685**
n=63	P	8.11 ± 6.77		-	0.468**
	P. goodeyi	9.30 ± 2.52			-
Petite Naine	RNI	3.56 ± 2.04	-	0.175	0.600**
n=90	P	5.93 ± 2.19		-	0.502**
	P. goodeyi	6.81 ± 4.20			-

*Data of flowered plants used; * p<0.05; ** p<0.01; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; RNI: (square root- transformed) root necrosis index; St. deviation: standard deviation;*

Pratylenchus goodeyi population densities were positively and significantly correlated with the RNI of Banane Cochon, Essong and Petite Naine. In more fertile soils, soil P content was significantly correlated with the RNI only on Essong. Although soil P content correlated positively with the observed RNI on Essong (Table 3.33), soil P content did not significantly contribute to the models for any of the cultivars. The results of the standard multiple regression analysis of RNI on *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.34. The models obtained were significant for all three cultivars ($p<0.01$): between 29% and 46% of the observed variation in RNI at flowering could be explained using *P. goodeyi* root population densities and soil P content. *Pratylenchus goodeyi* root population density was the best unique predictor variable in each cultivar's model and positively correlated with the observed RNI (for Banane Cochon ß = 0.55; for Essong = 0.63; for Petite Naine ß = 0.68; $p<0.01$).

Table 3.34: Regression of (square root transformed) root necrosis index (RNI) at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* population densities at flowering and soil P content in relatively more fertile soil.

Cultivar		b	ß
Banane	Intercept	1.73**	
Cochon	P	-0.01	-0.01
	P. goodeyi	0.30**	0.55**
	R^2	0.31	
	Adj. R^2	0.29	
	Std. Error of the Estimate	1.70	
	p-value	**	
Essong	Intercept	0.21	
	P	0.04	0.13
	P. goodeyi	0.55**	0.63**
	R^2	0.48	
	Adj. R^2	0.46	
	Std. Error of the Estimate	1.61	
	p-value	**	
Petite	Intercept	2.22**	
Naine	P	-0.16	-0.17
	P. goodeyi	0.33**	0.68**
	R^2	0.38	
	Adj R^2	0.37	
	Std. Error of the Estimate	1.91	
	p-value	**	

*Data of flowered plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj.* R^2*: model adjusted* R^2*; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3.6 Root necrosis index regressed on *Pratylenchus goodeyi* population densities and soil P content in less fertile soils

The descriptive statistics and correlations of the root necrosis index (RNI) with soil P content and (ln-transformed) *P. goodeyi* population densities in less fertile soils are given in Table 3.35.

Table 3.35: Correlations between (square root-transformed) root necrosis index (RNI) of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively less fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	RNI	P	*P. goodeyi*
Banane Cochon	RNI	6.08 ± 1.88	-	0.404*	0.350*
n=29	P	3.13 ± 0.58		-	0.302
	P. goodeyi	10.61 ± 2.21			-
Essong	RNI	7.13 ± 1.91	-	0.103	0.703**
n=20	P	3.65 ± 0.17		-	0.249
	P. goodeyi	10.51 ± 2.83			-
Petite Naine	RNI	5.90 ± 1.95	-	-0.119	0.247*
n=47	P	3.45 ± 0.58		-	-0.076
	P. goodeyi	11.04 ± 0.85			-

*Data of flowered plants used; * p<0.05; ** p<0.01; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; RNI: (square root- transformed) root necrosis index; Std. deviation: standard deviation;*

Only moderate positive correlations were observed between the RNI in less fertile soils on Banane Cochon and Petite Naine and *P. goodeyi* root population densities at flowering ($p<0.05$; Table 3.35). The results of the standard multiple regression analysis of RNI on *P. goodeyi* population densities and soil P content in relatively less fertile soils are given in Table 3.36. Soil P content and *P. goodeyi* population densities at flowering were unable to explain any of the variation observed in RNI on Petite Naine (Table 3.36). Both variables explained a small fraction of the variation observed in RNI on Banane Cochon when simultaneously entered into the model (Adjusted $R^2 = 0.16$, $p<0.05$), however, neither soil P content nor *P. goodeyi* root population densities alone contributed significantly to this model, indicating that the joint contribution accounted for some, but only minor variation. In less fertile soils, a larger proportion of the variation in RNI on Essong could be explained using soil P content and *P. goodeyi* (Adjusted $R^2 = 0.44$, $p<0.05$). *Pratylenchus goodeyi* population densities was the best unique predictor in this model (ß = 0.72) and

a strong positive correlation between RNI and *P. goodeyi* root population densities was observed for Essong in less fertile soils (r = 0.703, p<0.01; Tables 3.35 and 3.36).

Table 3.36: Regression of (square root transformed) root necrosis index (RNI) at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* root population densities at flowering and soil P content in relatively less fertile soil.

Cultivar		b	ß
Banane	Intercept	0.49	
Cochon	P	1.06	0.33
	P. goodeyi	0.21	0.25
	R^2	0.22	
	Adj. R^2	0.16	
	Std. Error of the Estimate	1.72	
	p-value	*	
Essong	Intercept	5.10	
	P	-0.84	-0.08
	P. goodeyi	0.49**	0.72**
	R^2	0.50	
	Adj. R^2	0.44	
	Std. Error of the Estimate	1.42	
	p-value	*	
Petite	Intercept	0.99	
Naine	P	-0.46	-0.14
	P. goodeyi	0.59	0.26
	R^2	0.08	
	Adj. R^2	0.39	
	Std. Error of the Estimate	1.91	
	p-value	ns	

*Data of flowered plants used; * p<0.05; ** p<0.01; P: soil P content (ppm); P. goodeyi: root population densities of (ln-transformed) Pratylenchus goodeyi/100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3.7 Non-damaged root index regressed on Pratylenchus goodeyi population densities and soil P content in more fertile soils

The descriptive statistics and correlations of the non-damaged root index (NDRI) with soil P content and (ln-transformed) *P. goodeyi* population densities in more fertile soils are given in Table 3.37. *Pratylenchus goodeyi* population densities were significantly and negatively correlated with the NDRI of all three cultivars, whereas, the soil P content was significantly correlated with the NDRI of Banane Cochon and Essong but not with the NDRI of Petite Naine.

Table 3.37: Correlations between the non-damaged root index (NDRI) of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively more fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	NDRI	P	*P. goodeyi*
Banane Cochon	NDRI	1570.1 ± 924.7	-	0.327**	-0.638**
n=76	P	7.43 ± 3.35		-	-0.238*
	P. goodeyi	7.33 ± 3.75			-
Essong	NDRI	735.6 ± 440.3	-	-0.302**	-0.662**
n=63	P	8.11 ± 6.77		-	0.468**
	P. goodeyi	9.30 ± 2.52			-
Petite Naine	NDRI	1639.6 ± 837.1	-	-0.101	-0.541**
n=90	P	5.93 ± 2.19		-	0.502**
	P. goodeyi	6.81 ± 4.20			-

*Data of flowered plants used; * p<0.05; ** p<0.01; NDRI: Non-damaged root index; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi per *100g fresh root weight; std. deviation: standard deviation.*

The results of the standard multiple regression analysis of the NDRI on *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.38. Between 32% and 42% of the variation observed in the NDRI at flowering could be explained using soil P content and *P. goodeyi* population densities (Table 3.38). *Pratylenchus goodeyi* population density was the best unique predictor variable in the multiple regression models for NDRI on all cultivars (Table 3.38). Soil P content contributed significantly to the observed variation in NDRI for Banane Cochon and Petite Naine, but not for Essong (Table 3.38).

Table 3.38: Regression of the non-damaged root index (NDRI) at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* population densities at flowering and soil P content in relatively more fertile soil.

Cultivar		b	ß
Banane	Intercept	2262.08**	
Cochon	P	51.21*	0.19*
	P. goodeyi	-146.43**	-0.59**
	R^2	0.44	
	Adj. R^2	0.42	
	Std. Error of the Estimate	701.90	
	p-value	**	
Essong	Intercept	1873.76**	
	P	0.63	0.01
	P. goodeyi	-116.53**	-0.67**
	R^2	0.44	
	Adj. R^2	0.42	
	Std. Error of the Estimate	335.57	
	p-value	**	
Petite	Intercept	2014.53**	
Naine	P	86.78*	0.23*
	P. goodeyi	-130.54**	-0.66**
	R^2	0.33	
	Adj. R^2	0.32	
	Std. Error of the Estimate	692.23	
	p-value	**	

*Data of flowered plants used; * p<0.05; ** p<0.01; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3.8 Non-damaged root index regressed on *Pratylenchus goodeyi* population densities and soil P content in less fertile soils

The descriptive statistics and correlations of the non-damaged root index (NDRI) with soil P content and (ln-transformed) *P. goodeyi* population densities in less fertile soils are given in Table 3.39. *Pratylenchus goodeyi* population densities were negatively correlated with NDRI of both Essong and Banane Cochon plants in less fertile soils (for Banane Cochon r = -0.529; for Essong r = -0.539; $p<0.01$).

Table 3.39: Correlations between the non-damaged root index (NDRI) of Banane Cochon, Essong and Petite Naine at flowering, (ln-transformed) *Pratylenchus goodeyi* population densities and soil P content in relatively less fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	NDRI	P	*P. goodeyi*
Banane Cochon	NDRI	719.9 ± 420.2	-	-0.390*	-0.529**
n=29	P	3.13 ± 0.58		-	0.302
	P. goodeyi	10.61 ± 2.21			-
Essong	NDRI	574.0 ± 438.0	-	-0.172	-0.539**
n=20	P	3.65 ± 0.17		-	0.249
	P. goodeyi	10.51 ± 2.83			-
Petite Naine	NDRI	871.6 ± 571.4	-	0.036	-0.145
n=47	P	3.45 ± 0.58		-	-0.076
	P. goodeyi	11.04 ± 0.85			-

*Data of flowered plants used; * p<0.05; ** p<0.01; NDRI: Non-damaged root index; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi per *100g fresh root weight; std. deviation: standard deviation*

The results of the standard multiple regression analysis of the NDRI on *P. goodeyi* population densities and soil P content in relatively less fertile soils are given in Table 3.40. Whereas the multiple regression model failed to explain any of the variation observed in NDRI of Petite Naine plants at flowering (Table 3.40), these models were significant for Banane Cochon and Essong. *Pratylenchus goodeyi* population density was the best unique predictor for NDRI for these two cultivars (for Banane Cochon ß = -0.45; for Essong ß = -0.53; $p<0.05$; Table 3.40). In less fertile soils, the soil P content did not contribute significantly to the observed variation of NDRI for any of the three cultivars (Table 3.40).

Table 3.40: Regression of the non-damaged root index (NDRI) at flowering of three *Musa* cultivars on (ln-transformed) *Pratylenchus goodeyi* root population densities at flowering and soil P content in relatively less fertile soil.

Cultivar		b	ß
Banane	Intercept	2206.87**	
Cochon	P	-183.15	-0.25
	P. goodeyi	-86.03*	-0.45*
	R^2	0.34	
	Adj. R^2	0.29	
	Std. Error of the Estimate	354.70	
	p-value	**	
Essong	Intercept	1800.88	
	P	-100.49	-0.04
	P. goodeyi	-81.79*	-0.53*
	R^2	0.29	
	Adj. R^2	0.21	
	Std. Error of the Estimate	389.67	
	p-value	*	
Petite	Intercept	1810.78	
Naine	P	46.20	-0.05
	P. goodeyi	-99.46	-0.15
	R^2	0.02	
	Adj. R^2	-0.02	
	Std. Error of the Estimate	577.42	
	p-value	ns	

*Data of flowered plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj.* R^2*: model adjusted* R^2*; Std. Error of the estimate: standard error of the estimate.*

3.4.2.4 Effect of soil P content, the number of dead roots at flowering and the non-damaged root index on bunch weight

3.4.2.4.1 Bunch weight regressed on the number of dead roots, the non-damaged root index (NDRI) and soil P content in more fertile soils

The descriptive statistics and correlations of bunch weight with soil P content, the number of dead roots and the NDRI of plants in more fertile soils are given in Table 3.41.

Table 3.41: Correlations between bunch weight, the number of dead roots and the non-damaged root index (NDRI) of Banane Cochon, Essong and Petite Naine at flowering and soil P content in relatively more fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Bunch weight	P	Dead roots	NDRI
Banane Cochon	Bunch weight	15.23 ± 5.24	-	0.519**	0.191	0.459**
n=71	P	7.56 ± 3.43		-	0.266*	0.303*
	Dead roots	2.44 ± 2.84			-	-0.192
	NDRI	1646.06 ± 908.02				-
Essong	Bunch weight	25.22 ± 8.60	-	0.600**	0.144	0.018
n=47	P	8.01 ± 6.66		-	0.321**	-0.260*
	Dead roots	1.00 ± 1.35			-	-0.501**
	NDRI	706.79 ± 428.01				-
Petite Naine	Bunch weight	15.21 ± 3.65	-	0.218*	-0.070	0.358**
n=86	P	5.91 ± 2.20		-	0.086	-0.089
	Dead roots	2.02 ± 2.52			-	-0.030
	NDRI	1675.69 ± 836.45				-

*Data of harvested plants used; * $p<0.05$; ** $p<0.01$; bunch weight in kg; P: soil P content (ppm); Dead roots: number of dead roots; NDRI: non-damaged root index; std. deviation: standard deviation.*

The NDRI on Banane Cochon and Petite Naine plants was positively correlated with the bunch weight, whereas the number of dead roots was not significantly correlated with the bunch weight on either of these two cultivars. For Essong, neither the number of dead roots nor the NDRI was correlated with the bunch weight. On all three cultivars a positive correlation was observed between soil P content and bunch weight.

The results of the standard multiple regression analysis of bunch weight on soil P content, the number of dead roots and NDRI in relatively more fertile soils are given in Table 3.42. Between 17% and 37% of the variation observed in bunch weight of harvested plants could be explained using the following three predictor variables: the number of dead roots, NDRI and soil P content.

Table 3.42: Regression of bunch weight of three *Musa* cultivars on the number of dead roots, the non-damaged root index (NDRI) at flowering and soil P content in relatively more fertile soils.

Cultivar		b	ß
Banane	Intercept	6.68	
Cochon	P	0.55**	0.36**
	Dead roots	0.31	0.17
	NDRI	0.002**	0.38**
	R^2	0.40	
	Adjusted R^2	0.37	
	Std. Error of the Estimate	4.17	
	p-value	**	
Essong	Intercept	15.45	
	P	0.83**	0.64**
	Dead roots	0.26	0.04
	NDRI	0.004	0.20
	R^2	0.39	
	Adjusted R^2	0.35	
	Std. Error of the Estimate	6.93	
	p-value	**	
Petite	Intercept	10.15	
Naine	P	0.43*	0.23*
	Dead roots	-0.12	-0.08
	NDRI	0.002**	0.38**
	R^2	0.20	
	Adjusted R^2	0.17	
	Std. Error of the Estimate	3.33	
	p-value	**	

*Data of harvested plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm); Dead roots: number of dead roots; NDRI: Non-damaged root index; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

The number of dead roots, however, did not contribute significantly to the multiple regression model or significantly correlate with the bunch weight of any of the three cultivars (Tables 3.41 and 3.42). The single best predictor

variable for the bunch weight of Banane Cochon and Petite Naine was the NDRI (for Banane Cochon ß = 0.38, for Petite Naine ß = 0.38; $p<0.01$; Table 3.42). NDRI did not contribute to the regression model for Essong however, where soil P was instead the best unique predictor variable (ß = 0.64, $p<0.01$). Soil P content also contributed to the models for bunch weight of the other two cultivars, but less than was seen for NDRI (for Banane Cochon ß = 0.36, for Petite Naine ß = 0.23; $p<0.01$).

3.4.2.4.2 Bunch weight regressed on the number of dead roots, the non-damaged root index (NDRI) and soil P content in less fertile soils

The descriptive statistics and correlations of bunch weight with soil P content, the number of dead roots and the NDRI of plants in less fertile soils are given in Table 3.43. No significant correlations between bunch weight and the number of dead roots were observed (Table 3.43).

Table 3.43: Correlations between bunch weight, the number of dead roots and the non-damaged root index (NDRI) of Banane Cochon, Essong and Petite Naine at flowering and soil P content in relatively less fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Bunch weight	P	Dead roots	NDRI
Banane Cochon	Bunch weight	10.34 ± 3.49	-	-0.334	0.158	0.435*
n=20	P	3.18 ± 0.60		-	-0.342	-0.391
	Dead roots	2.90 ± 3.81			-	-0.273
	NDRI	680.50 ± 438.50				-
Essong	Bunch weight	18.47 ± 8.28	-	0.198	-0.065	0.625*
n=11	P	3.59 ± 0.16		-	0.068	-0.267
	Dead roots	0.82 ± 1.25			-	-0.582*
	NDRI	454.52 ± 462.05				-
Petite Naine	Bunch weight	13.53 ± 3.99	-	0.033	0.017	0.167
n=39	P	3.45 ± 0.62		-	0.104	0.035
	Dead roots	2.62 ± 3.51			-	-0.027
	NDRI	931.03 ± 596.82				-

*Data of harvested plants used; * $p<0.05$; ** $p<0.01$; bunch weight in kg; P: soil P content (ppm); Dead roots: number of dead roots; NDRI: non-damaged root index; std. deviation: standard deviation.*

The results of the standard multiple regression analysis of bunch weight on soil P content, the number of dead roots and NDRI in relatively less fertile soils are

given in Table 3.44. Fifty-eight percent of the variation observed in bunch weight for Essong could be explained using this multiple regression model. The best unique predictor variable for bunch weight of Essong was the NDRI (ß = 1.04, $p<0.05$).

Table 3.44: Regression of bunch weight of three *Musa* cultivars on the number of dead roots, the non-damaged root index (NDRI) at flowering and soil P content in relatively less fertile soils.

Cultivar		b	ß
Banane	Intercept	7.81	
Cochon	P	-0.28	-0.05
	Dead roots	0.25	0.28
	NDRI	0.004	0.49
	R^2	0.27	
	Adj. R^2	0.14	
	Std. Error of the Estimate	3.24	
	p-value	ns	
Essong	Intercept	-73.50	
	P	22.46	0.44
	No. of dead roots	3.38	0.51
	NDRI	0.019*	1.04*
	R^2	0.70	
	Adj. R^2	0.58	
	Std. Error of the Estimate	5.39	
	p-value	*	
Petite	Intercept	11.88*	
Naine	P	0.16	0.03
	No. of dead roots	0.02	0.02
	NDRI	0.001	0.17
	R^2	0.03	
	Adj. R^2	-0.05	
	Std. Error of the Estimate	4.09	
	p-value	ns	

*Data of harvested plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm); Dead roots: number of dead roots; NDRI: Non-damaged root index; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

The multiple regression models obtained for Banane Cochon and Petite Naine failed to explain any of the variation observed in bunch weight on less fertile soils (Table 3.44). The number of dead roots and soil P content did not

contribute significantly to the variation observed in the bunch weight of any of the three cultivars (Table 3.44).

3.4.2.5 Effect of soil P content and *Pratylenchus goodeyi* population densities on bunch weight

3.4.2.5.1 Bunch weight regressed on *Pratylenchus goodeyi* population densities and soil P content in more fertile soils

The descriptive statistics and correlations of bunch weight with *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.45. Significant positive correlations were found between bunch weight and soil P content for all cultivars ($p<0.05$). Significant negative correlations were found between bunch weight and (ln-transformed) *P. goodeyi* population densities for Banane Cochon and Petite Naine ($p<0.01$), but not for Essong.

Table 3.45: Correlations between bunch weight, (ln-transformed) *P. goodeyi* population densities and soil P content of Banane Cochon, Essong and Petite Naine in relatively more fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Bunch weight	P	*P. goodeyi*
Banane Cochon	Bunch weight	15.23 ± 5.24	-	0.519**	-0.302**
n=71	P	7.56 ± 3.43		-	-0.223
	P. goodeyi	7.33 ± 3.75			-
Essong	Bunch weight	25.22 ± 8.60	-	0.600**	0.173
n=47	P	8.01 ± 6.66		-	0.423**
	P. goodeyi	9.30 ± 2.52			-
Petite Naine	Bunch weight	15.21 ± 3.65	-	0.218*	-0.354**
n=86	P	5.91 ± 2.20		-	0.508**
	P. goodeyi	6.81 ± 4.20			-

*Data of harvested plants used; * p<0.05; ** p<0.01; bunch weight in kg; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; std. deviation: standard deviation.*

The results of the standard multiple regression analysis of bunch weight on *P. goodeyi* population densities and soil P content in relatively more fertile soils are given in Table 3.46.

Table 3.46: Regression of bunch weight of three *Musa* cultivars on (ln-transformed) *P. goodeyi* root population densities at flowering and soil P content in relatively more fertile soil.

Cultivar		b	ß
Banane	Intercept	11.65**	
Cochon	P	0.72**	0.48**
	P. goodeyi	-0.27	-0.20
	R^2	0.31	
	Adj. R^2	0.29	
	Std. Error of the Estimate	4.43	
	p-value	**	
Essong	Intercept	21.69**	
	P	0.83**	0.64**
	P. goodeyi	-0.33	-0.98
	R^2	0.37	
	Adj. R^2	0.34	
	Std. Error of the Estimate	7.00	
	p-value	**	
Petite	Intercept	13.56**	
Naine	P	0.89**	0.54**
	P. goodeyi	-0.54**	-0.63**
	R^2	0.34	
	Adj. R^2	0.32	
	Std. Error of the Estimate	3.00	
	p-value	**	

*Data of harvested plants used; * $p<0.05$; ** $p<0.01$; P: soil P content (ppm); P. goodeyi: root population densities of (ln-transformed) Pratylenchus goodeyi/100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate*

Around 30% of the variability in bunch weights of each cultivar could be explained using *P. goodeyi* population densities and soil P content. For Banane Cochon and Essong, soil P content was a better unique predictor than the (ln-transformed) population density of *P. goodeyi* (for Banane Cochon, ß = 0.48; for Essong, ß = 0.64, $p<0.01$). For the bunch weight of Petite Naine, *P. goodeyi* population density was the best unique predictor (ß = -0.63, $p<0.01$), although the difference with soil P content was minimal (ß = 0.54, $p<0.01$).

3.4.2.5.2 Bunch weight regressed on nematode root population densities and soil P content in less fertile soils

The descriptive statistics and correlations of bunch weight with *P. goodeyi* population densities and soil P content in relatively less fertile soils are given in Table 3.47.

Table 3.47: Correlations between bunch weight, (ln-transformed) *P. goodeyi* population densities and soil P content of Banane Cochon, Essong and Petite Naine in relatively less fertile soils of the experimental site.

Cultivar		Mean ± std. deviation	Bunch weight	P	*P. goodeyi*
Banane Cochon	Bunch weight	10.34 ± 3.49	-	-0.334	0.111
n=20	P	3.18 ± 0.60		-	0.359
	P. goodeyi	10.61 ± 2.21			-
Essong	Bunch weight	18.47 ± 8.28	-	0.198	-0.612*
n=11	P	3.59 ± 0.16		-	0.222
	P. goodeyi	10.51 ± 2.83			-
Petite Naine	Bunch weight	13.53 ± 3.99	-	0.033	-0.073
n=39	P	3.45 ± 0.62		-	0.018
	P. goodeyi	11.04 ± 0.85			-

*Data of harvested plants used; * p<0.05; ** p<0.01; bunch weight in kg; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; std. deviation: standard deviation.*

A significant negative correlation between Essong bunch weight and *P. goodeyi* population densities was also observed ($p<0.05$). No significant correlations of bunch weight with *P. goodeyi* population densities or soil P content were observed for Banane Cochon or Petite Naine.

The results of the standard multiple regression analysis of bunch weight on *P. goodeyi* population densities and soil P content in relatively less fertile soils are given in Table 3.48. Soil P content and (ln-transformed) *P. goodeyi* population densities were unable to explain bunch weight variation for any of the three cultivars.

Table 3.48: Regression of bunch weight of three *Musa* cultivars on (ln-transformed) *P. goodeyi* root population densities at flowering and soil P content in relatively less fertile soil.

Cultivar		b	ß
Banane	Intercept	14.40*	
Cochon	P	-2.49	-0.43
	P. goodeyi	0.36	0.27
	R^2	0.17	
	Adj. R^2	0.08	
	Std. Error of the Estimate	3.35	
	p-value	ns	
Essong	Intercept	12.03	
	P	17.93	0.35
	P. goodeyi	-3.06*	-0.69*
	R^2	0.49	
	Adj. R^2	0.37	
	Std. Error of the Estimate	6.59	
	p-value	ns	
Petite	Intercept	16.37	
Naine	P	0.22	0.03
	P. goodeyi	-0.33	-0.07
	R^2	0.006	
	Adj. R^2	-0.05	
	Std. Error of the Estimate	4.08	
	p-value	ns	

*Data of harvested plants used; * p<0.05; ** p<0.01; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi*/100g fresh root weight; Adj. R^2: model adjusted R^2; Std. Error of the estimate: standard error of the estimate.*

3.4.2.3 Summary of Results Part II

An overview of the results of the multiple regression analyses for each cultivar are given in the following three Tables (Tables 3.49a, 3.49b and 3.49c).

Table 3.49a: Summary of the multiple regression results for Banane Cochon.

	Dependent variables									
Predictor variables	Dead roots		Functional roots		RNI		NDRI		Bunch weight	
Nematodes and soil	MF	LF	MF	LF	MF	LF	MF	LF	MF	LF
P	++	°	+	°	°	°	+	°	++	°
P. goodeyi	°	°	--	°	++	°	--	--	-	°
Adj R^2	0.04	0.06	0.34	0.10	0.29	0.16	0.42	0.29	0.29	0.08
p	ns	ns	**	ns	**	*	**	*	**	ns
Soil and roots									MF	LF
P									+	°
Dead roots									°	°
NDRI									++	++
Adj R^2									0.37	0.14
p									**	ns

'+': predictor variable is positively correlated with dependent variable and contributes significantly to the model; '++': predictor variable is positively correlated and the best unique predictor; '-': predictor variable is negatively correlated with dependent variable and contributes significantly to model; '--': predictor variable is negatively correlated and the best unique predictor; '°': predictor variable does not contribute significantly to the model; '': F-test of the model is significant at p<0.05; '**': F-test of the model is significant at p<0.01; 'ns': model is not significant at p<0.05; MF: relatively more fertile soils; LF: relatively less fertile soils; P: soil P content (ppm);* P. goodeyi: *root population densities of* (*ln-transformed)* Pratylenchus goodeyi/*100g fresh root weight; Adj. R^2: model adjusted R^2; dead and functional roots: number of dead and functional roots at flowering; Bunch weight: in kg; RNI: (square root-transformed) root necrosis index (%); NDRI: non-damaged root index.*

Table 3.49b: Summary of the multiple regression results for Essong.

	Dependent variables									
Predictor variables	Dead roots		Functional roots		RNI		NDRI		Bunch weight	
Nematodes and soil	MF	LF	MF	LF	MF	LF	MF	LF	MF	LF
P	°	°	°	°	°	°	°	°	++	°
P.goodeyi	++	°	--	°	++	++	--	--	°	--
Adj R^2	0.24	-0.09	0.09	-0.04	0.46	0.44	0.42	0.21	0.34	0.37
p	**	ns	*	ns	**	**	**	*	**	ns
Soil and roots									MF	LF
P									++	°
Dead roots									°	°
NDRI									°	++
Adj R^2									0.35	0.58
p									**	**

Legend as in table 3.49a

Table 3.49c: Summary of the multiple regression results for Petite Naine.

	Dependent variables									
Predictor variables	Dead roots		Functional roots		RNI		NDRI		Bunch weight	
Nematodes and soil	MF	LF	MF	LF	MF	LF	MF	LF	MF	LF
P	°	°	°	°	°	°	+	°	+	°
P.goodeyi	++	°	--	°	++	°	--	°	--	°
Adj R^2	0.04	-0.03	0.16	-0.04	0.37	0.04	0.32	-0.02	0.32	-0.05
p	*	ns	**	ns	**	ns	**	ns	**	ns
Soil and roots									MF	LF
P									+	°
Dead roots									°	°
NDRI									++	°
Adj R^2									0.17	-0.05
p									**	ns

Legend as in table 3.49a

3.5 Discussion

3.5.1 Effect of field history on nematode population densities in the soil and soil chemical properties

Fourteen years after the previous experiment had been abandoned, the old *Musa* mats in the high nematode pressure (HNP) field consisted of many suckers (3125 corms/ha) whereas in the medium nematode pressure (MNP) field lower plant densities were observed (1625 corms/ha). The nematode population densities in the roots of the remaining *Musa* mats from these two fields did not differ significantly (mean: 18889 nematodes per 100g FRW). The low nematode pressure (LNP) field had no old *Musa* mats.

Nematode pressure could therefore be defined using the number of previous *Musa* mats. The effect of nematode infestation was confounded, however, by the effect of soil chemical properties, as the field with the highest nematode pressure (HNP) also had the lowest availability of soil macronutrients.

Bananas and plantains assimilate large amounts of nutrients from the soil (Lahav, 1995) and constitute a rich source of nutrients when used as mulch. By 1 YAP, when soil was sampled, the previous *Musa* mats would have decomposed (Delvaux, 1995; Lekasi *et al.*, 2001). Notwithstanding the larger quantity of mulch from the old *Musa* mats in the HNP field, soil chemistry values were consistently lower compared to the MNP or LNP field.

No effect of cultivar was observed for any of the soil variables, indicating that cultivar-related differences in nutrient uptake (Tézenas du Montcel and Skinner, 1987; Lahav, 1995) were subordinate to differences between field types at 1 YAP and that cultivars within the same field (HNP, MNP or LNP) were subject to similar nutrient availability. The combined effect of soil chemistry and nematode pressure made it difficult, however, to separate the effect of nematodes from soil chemical properties using analysis of variance (ANOVA).

Field history had a significant effect on most parameters observed during this experiment. No interaction effects of field history x cultivar were observed, indicating that the cultivars were affected in a similar way by field history, albeit in differing degrees of severity.

3.5.2 Effect of field history on nematode population densities in the roots and species composition

The impact of agricultural practices on nematode population densities and community structure is well documented (see for instance Ferris and Ferris, 1974; Freckman and Caswell, 1985; Yeates and Bongers, 1999). The wide host range exhibited by some nematode species and their ability to persist on poor

plant hosts leads to relatively slow changes in soil nematode community structures during fallow periods, dependent on the succession of vegetation (Cadet *et al.*, 2005). Conversely, changes can occur rapidly once cultivation is resumed (Villenave *et al.*, 2001), owing to the short life cycle of most plant-parasitic nematodes. Hodda *et al.* (1997) found after clearance of a tropical forest in southern Cameroon, that the total biomass of plant-parasitic nematodes increased, whereas that of free-living nematodes decreased, when the soil was used for agriculture.

Changes in the nematode community structure during the current experiment are best illustrated by nematode infection levels in roots of *Musa* mats in the LNP field. At 1 YAP, root populations of *P. goodeyi* and other nematodes had accumulated to 4518 nematodes per 100 g FRW on plants in the LNP field, whereas total nematode population densities in the HNP and MNP fields already exceeded those found in the roots of the previous *Musa* mats (> 30000 nematodes per 100 g FRW).

Nematode population densities can accumulate rapidly in the presence of a suitable host (McSorley, 1998) and by flowering total root nematode population densities in the LNP field had accumulated to levels similar to those in the other fields at 1 YAP (24815 nematodes per 100 g FRW). These population densities remained significantly lower than those found on flowering plants in the HNP and MNP fields (> 60000 nematodes per 100 g FRW).

Assuming stable nematode multiplication rates, lower infection levels until the first ratoon might be expected in the LNP field. Roots of *in vitro* plantlets are known to be more susceptible to early nematode infection than the thicker roots of sucker-derived plants (De Waele *et al.*, 1998; Blomme *et al.*, 2000). This can be explained due to an 8-week delay[1] in the growth of the root system of *in vitro* plantlets when planted in the field in conjunction with the more fragile anatomical structure of the newly formed root system (Stoffelen, 2000; Swennen, personal communication). It may therefore be possible to attain an even longer period of relatively low nematode infestation levels if suckers are used instead of *in vitro* planting material.

The use of clean planting material, in the form of hot-water treated suckers (Colbran and Saunders, 1967) or *in vitro* plantlets, is often advocated to reduce nematode-related damage to bananas and plantains (Tenkouano *et al.*, 2006). Predictably, the efficacy of this practice is reduced when clean planting material is (inter)planted into an infested field (Speijer *et al.*, 2000; Speijer *et al.*, 2001b; Elsen *et al.*, 2004), as was seen for plants in the HNP and MNP fields.

[1] Root growth of *in vitro* plantlets starts after an initial lag phase of 4 weeks. Flushes of new primary roots occur at 4 and 8 weeks after planting (Stoffelen, 2000).

At 1 YAP, 32% of all nematodes in the LNP field were *P. goodeyi* compared to 75% at flowering. Conversely, where *Musa* mats had existed prior to experiment establishment *P. goodeyi* was the most prevalent nematode species at all sampling times.

Meloidogyne spp. predominated samples from the LNP field at 1 YAP, but were only marginally represented in root samples from the other two field types. *Meloidogyne* spp. are known to exhibit a wide host range (CABI, 2002) which would have allowed them to build up significant population densities during the fallow phase. *Pratylenchus goodeyi* on the other hand has a comparatively narrow host range and *Musa* spp. are a preferred host (Pinochet *et al.*, 1998), thus explaining the rapid multiplication of *P. goodeyi* after *in vitro* plantlets were planted in a previously *Musa*-free field. Interspecific competition between *Pratylenchus* spp. and *Meloidogyne* spp. has also been observed (Melakeberhan and Dey, 2003), whereby migratory nematodes tend to suppress sedentary nematode species in the tropics due to a higher multiplication rate of the former (Pinochet, 1996).

Pratylenchus goodeyi is considered indigenous to eastern Africa (Gowen *et al.*, 2005) and some native African plant species have been identified as suitable hosts in East Africa (Mbwana *et al.*, 1995; Namaganda *et al.*, 2000; Prasad *et al.*, 2000). Several of these plant species are also found in Cameroon (Price, 2006) and the argument can be made that *P. goodeyi* is indigenous to African highland regions in general, thus exhibiting an afro-montane distribution (Price and Bridge, 1995).

No *Musa* mats or other food crops were found in the LNP field prior to trial establishment. Soil sampled in the LNP field prior to planting revealed that *P. goodeyi* was present in the soil at population densities comparable to those found in the MNP and HNP fields. This corroborates Prasad *et al.* (2000), who suggested that at least part of the natural vegetation can support residual populations or that eggs of *P. goodeyi* can survive in diapause in the soil in absence of a suitable host.

Although quiescent periods are more common for sedentary parasites, other lesion nematodes, such as *Pratylenchus penetrans*, a parasite of potato, can survive in dormancy by slowing their metabolism and activity in response to environmental stress (Townshend, 1984; Ferris and Ferris, 1998; McSorley, 2003).

3.5.3 Effect of field history on plant growth

No effect of field history was seen on weekly plant growth rates from 1-6 MAP and few significant differences among the field types were observed in the plant growth measurements taken during this period.

One exception was the circumference of plants, which at 1 MAP was largest in the HNP field. Plants in the HNP field were also numerically taller at 1 MAP, although the difference with heights of plants in the other field types was not significant at $p<0.05$. This first month of plant growth coincided with the start of the dry season in 2003. It is plausible that the increased mulch, from previous *Musa* mats in the HNP field, provided some solace for these plants.

Lekasi *et al.* (2001) studied the decomposition of banana mulch in Uganda and found a 50% decomposition for the pseudostem, including roots and corm, after 33 days during the rainy season (decomposition of leaves took longer). Decomposition rates during tropical dry seasons are generally slower than those observed during rainy seasons (Thomas and Asakawa, 1993; Gijsman *et al.*,1997). Thus plants in the HNP field could have benefited from increased soil water retention due to this mulch before the adverse effects of nematode infection became a constraint, giving them a small advantage over plants in other fields.

Mean weekly plant growth rates were affected by field history, however, with higher leaf emission rates and incremental change in height and circumference in the LNP field, and by 1 YAP the effect of nematode pressure was apparent. In the HNP field, fewer leaves, smaller circumference and fewer suckers were observed compared to plants in the other two field types. Plants were also numerically shortest in the HNP field, although the difference with the height of plants from the other two fields was insignificant. These results contradict those of McIntyre *et al.* (2000), who found no effect of nematode infection on aboveground biomass. However, in the study by McIntyre *et al.* (2000) the effect of mulching and nematode inoculation were jointly analyzed. As mulching significantly increased biomass, it may be that the joint analysis of both factors obscured the effect of the factor with less impact.

At flowering, most phenotypic differences between field types were not significant at the 0.05-level. The number of leaves produced at flowering is cultivar-specific (Swennen and Vuylsteke, 1987). The pseudostem is built of leaf sheaths thickly packed together (Simmonds, 1966), so plant height and circumference are related to the number of leaves produced (Ortiz and Vuylsteke, 1998; Crouch *et al.*, 2000). The growth of the mother plant ceases once flowering is initiated. So, genetic differences may partly explain the similarities at flowering among the field types in these vegetative parameters, as measurements were taken when plants flowered (12-28 MAP) and not at fixed time intervals.

In general, vigorous vegetative plant growth was associated with earlier flowering and heavier bunch weights, confirming previous reports (Swennen and De Langhe, 1985; Ortiz and Vuylsteke, 1998; Buah *et al.*, 2000). As plant

growth was more vigorous in the LNP field, plants flowered earlier. The strength of the correlations examined in this study varied among the three cultivars. The sign and significance of most correlations, however, remained the same. Cultivar-related variation in the strength of the relationship between vegetative growth and production parameters is well known (Swennen and De Langhe, 1985; Ortiz and Vuylsteke, 1998; Tenkouano *et al.*, 2002).

Not all vegetative parameters are equally useful indicators of productivity, as was illustrated by the negative correlation between the number of leaves produced and bunch weight for the cultivars in this study. This somewhat counterintuitive result can be understood by taking into account the late date of flowering for the cultivars at Mbouroukou (daily temperature 20°C). Indeed, in the current study Banane Cochon, Essong and Petite Naine took twice as long to flower and produced more leaves compared to similar cultivars evaluated at Onne (daily temperature 30°C) in 1998 by Ortiz and Vuylsteke (Table 3.50).

Table 3.50: Comparison of the date of flowering and number of leaves at flowering obtained by Ortiz and Vuylsteke (1998) with the values obtained during the current experiment.

Cultivar[1]	Date of flowering		Number of leaves at flowering	
	Source: Ortiz and Vuylsteke (1998)*	This study	Source: Ortiz and Vuylsteke (1998)*	This study
Banane Cochon	244	535	31	45
Essong	364	639	39	53
Petite Naine	202	481	25	44

**: management practices: fertilizer application and mulching, data from several growth cycles (Ortiz and Vuylsteke, 1998).*

Further inspection of the data showed that when the date of flowering was used as a control variable, a positive relationship existed between the number of leaves at flowering and bunch weight for Essong and Petite Naine. For Banane Cochon, controlling for the date of flowering, no significant correlation was found. Ortiz and Vuylsteke (1998) also did not always find a significant (positive) correlation between the number of leaves at flowering and bunch weight.

Environment is known to influence the total number of leaves produced and temperature is thought to contribute to this effect (Turner, 1995). Bunch weight

[1] The *Musa* cultivars used by Ortiz and Vuylsteke (1998) were: for cultivars classified as cooking banana (Bluggoe, Champa madras, Nzizi, Ayaba and Poovan), for cultivars classified as Cavendish (Dwarf Cavendish and Giant Cavendish – not further specified) and for cultivars classified as Giant French plantain (Apem Pa, Ebare Egome, Ntanga 2, Ntanga 5, Ntanga 6, Osabum and Ovang)

is dependent on the photosynthetic capacity of the plant, however, and it is the total leaf area, which is a function of the number of standing leaves, that determines this capacity. The total leaf area and leaf emission rate were both positively correlated with the bunch weight on all cultivars in this study. Plants with a higher leaf emission rate, almost always linked with lower leaf decay, will have a higher total leaf area and thus higher total dry matter production since heavier bunches are produced (Swennen and De Langhe, 1985). Also in concordance with Swennen and De Langhe (1985), earlier measurements of pseudostem height correlated more highly with bunch weight than the pseudostem height at flowering. This is to be expected considering that the height of plants measured at fixed time intervals is a function of the leaf emission rate. By contrast, the height measured at flowering depends on the total number of leaves produced.

The number of suckers produced at 1YAP and at flowering differed significantly among the field types confirming the flexibility of this trait to environmental factors (Ortiz and Vuylsteke, 1998). The highest number of suckers was found on plants in the MNP field, indicating that soil fertility played a more important role in suckering behavior of *Musa* plants than nematode infection. This is in line with a physiological study of suckering behaviour conducted by Swennen (1984). He found that gibberellic acid and cytokinin play a key role in suckering. Since both phytoregulators are formed in root tips, it follows that factors that stimulate root branching, such as soil fertility and mulching, may have a beneficial effect on the number of suckers produced (Swennen, 1984). Given that plant parasitic nematodes do not preferentially attack the root tips (Talwana, 2002), one could expect that a larger root system due to higher fertility might explain the larger number of suckers. While examination of the number of functional roots would appear to contradict this hypothesis, as the number of functional roots was highest in the LNP field, it is important to note that this only gives an estimate of the number of primary roots. No data was gathered on the number of secondary and tertiary roots (and their associated root tips). It is possible that plants in the MNP field showed a more intense secondary and tertiary branching of the roots.

Numerical differences in the vegetative growth index (VGI) per field type were observed, with higher VGI in the LNP field and lower VGI in the HNP field, however, these differences were not significant. The sucker growth index (SGI), which gives an indication of the development of the ratoon crop (Tenkouano *et al.*, 2007), also did not differ significantly among the field types. This may seem to contradict the observation that increased nematode pressure lengthened the growth cycle of the plant crop. However, although Tenkouano *et al.* (2007) found a negative correlation between the days to flowering of the ratoon crop

and SGI of the plant crop, the coefficient of determination was extremely low (R^2 = 0.087; calculated from r = -0.295; Tenkouano *et al.*, 2007). The SGI alone is therefore not a very good predictor for the date of flowering in ratoon crops. As the current experiment was terminated before the ratoon crops had flowered, speculation of the effect of field history on the ratoon crop is limited, especially where differences are slight.

The aboveground robustness of plants, as indicated by the pseudostem index, did not differ among the field types, suggesting that the susceptibility to topple was not proportionate to the bunch-supporting structure of the plant, but more likely due to a combination of root health characteristics and bunch weight.

At 1 YAP, the root necrosis index (RNI) was highest and the non-damaged root index (NDRI) lowest in the HNP field. At flowering, RNI and NDRI were highest and lowest, respectively, in both the MNP and HNP fields. Highest plant loss due to toppling was in the MNP field, however, and occurred mostly post-flowering from 18 MAP onwards. This coincides with the onset of the rainy season (and storms) in 2004. The combination of accumulated root damage in the MNP field and the fact that several plants had started flowering, thus carrying top-heavy bunch weights, explains the higher number of toppled plants in this field. Conversely, in the HNP field roots suffered similar damage, but less plants had flowered, while in the LNP field a similar number of plants had flowered, but less root damage was observed. In general, root system health was best for plants in the LNP field and worse for plants in the HNP field.

These results corroborate the results obtained by Speijer *et al.* (1999) from a field infested with *R. similis, H. multicinctus* and *P. goodeyi* (*R. similis* was the most prevalent species), where a higher percentage of toppled plants was observed in infested fields (7.5%) compared to non-infested fields (0.6%) over three cropping cycles (2^{nd}-4^{th} ratoon). Toppling occurred more frequently in ratoon plants when the mother plant had also toppled, as damage to roots and corm increased gradually with each successive cycle (Speijer *et al.*, 1999). This would suggest that the effect of nematode infection observed in the current experiment may also be carried through to successive crop cycles.

3.5.4 Effect of field history on weevil damage

The standard procedure to evaluate the effect of weevil damage in a *Musa* experiment uses assessments of each mother plant directly after harvest (Speijer and Gold, 1996). Alternatively, insecticide can be applied to control weevil populations, thus reducing their impact on yield to negligible levels. At the start of the current experiment, trapping revealed a low weevil population. This led to the, in hindsight erroneous, assumption that a single insecticide application (active ingredient: fipronil) could control the population.

Trapping can lead to an underestimation of the weevil population, because the size of the non-active weevil population is very variable (Messiaen, 2002). Additionally, considering the relatively long duration of the experiment, it is possible that some weevils survived the insecticide treatment and were able to rebuild their populations to damaging levels. Also, weevils from the untreated surrounding fields may have migrated towards the experiment. In any case, the single insecticide application was not sufficient to control the weevil population throughout the course of the current experiment. This oversight meant that many plants had already been harvested by the time it became apparent that weevil damage might be a contributing factor to yield loss. In retrospect it would have been better to either control the weevil population by reapplying the insecticide or to evaluate the weevil damage per plant at harvest. In order to acquire some knowledge of the potential damage caused by weevils in this experiment, an adaptation of the standard procedure was implemented: at the end of the experiment the accumulated damage caused by weevils over the course of 28 months was quantified. However, as this procedure differs from that commonly used by entomologists, a direct comparison with data from other studies is not possible.

In the current experiment, the number of mats showing some form of weevil damage in either the mother plant or lateral shoots differed per field type but was higher where nematode damage was highest. In the HNP and MNP fields, 63-71% of all mats were affected by weevil damage ranging from mild to more severe damage symptoms in the central cylinder or cortex, compared to 57% of the mats in the LNP field.

Speijer *et al.* (1993) reported higher weevil damage associated with nematode infected plants compared to non-infected plants. The field used for the current experiment was less than 1 ha in size. Considering the mobility of weevils and their ability to fly (Messiaen, 2002), there is no reason why weevil infestation should mirror that of nematodes. The higher percentage of weevil-infested plants where nematode damage was highest suggests both pests may interact. Speijer *et al.* (1999) proposed that corm softening by water stress induced by nematode infestation may favor weevil egg deposition, or alternatively, that weevil females may be more attracted to damaged *Musa* material, as was observed by Budenberg *et al.* (1993). As no correlation was found between the corm hardness of different *Musa* spp. and the percentage of weevil infestation or damage severity (Ortiz *et al.*, 1995), it appears likely that damaged tissue plays a more important role in weevil attraction.

The severity of infestation did not differ significantly among the field types, however. On infested mats, on average 1/8th of the cortex or corm of the mother plant, ratoon crop or lateral shoots had been affected. The severity of disease

expression is known to increase as plantations age (Rukazambuga *et al.*, 1998; Rukazambuga *et al.*, 2002). In Uganda for example, significant yield losses due to weevil damage did not appear until the 4th crop cycle (Gold *et al.*, 2004), suggesting that the impact of weevils during the course of this experiment may have been negligible.

3.5.5 Effect of field history on yield and yield loss

Nematode-related damage was proportionate to the nematode infection levels in the field. Relatively more attainable yield was lost to known effects of nematode damage (Gowen *et al.*, 2005) such as, toppling and lengthening of the growth cycle, in the fields where *Musa* mats had persisted during the fallow phase, with losses exceeding 65% of the attainable yield. Losses were more apparent in the number of plants that failed to reach harvest and less apparent in bunch weights, which did not differ significantly between fields. Fewer plants were harvested in the HNP field and more plants were harvested in the LNP field.

Similar observations have been made for commercial banana in *R. similis* infested soils. Chabrier and Quénéhervé (2003) found no difference in bunch weight of the plant crop between fields where more versus fewer bananas persisted during a 6-month fallow phase and a higher percentage of harvested plants where no bananas persisted. Likewise, Araya and De Waele (2005) also found no correlation between nematode population densities and bunch weight in nematode-infested soils in Costa Rica.

A two-fold difference in mean yield was observed between the highest and lowest yielding fields used in this experiment. In general, the mean yields obtained in the current experiment were not abnormally higher or lower than those reported in the literature.

Mean yields obtained for Essong (19.3 Mg/ha) in the current experiment were twice as high as those obtained for Essong in southern Cameroon, but similar plant losses, in terms of percentage lost, were observed (Hauser, 2000; Norgrove and Hauser, 2002). Essong bunch size was similar to that obtained for Giant French type plantain in Onne, Nigeria (Ortiz and Vuylsteke, 1998).

Mean yield obtained for Banane Cochon in the current experiment was 17.9 Mg/ha. Data from a fertilizer experiment in Uganda yielded between 3.1 and 18.9 Mg/ha/year for a cooking banana cultivar at altitudes where *P. goodeyi* is expected to be the dominant nematode species (Smithson *et al.*, 2004), but yields above 50 Mg/ha/year for cooking banana in Uganda have also been reported (Smithson *et al.*, 2001).

Ortiz and Vuylsteke (1998) calculated the "total yield potential"[1], using the mean bunch weights obtained after several cycles for 72 plantain and 18 banana cultivars in a field experiment in Onne, Nigeria, where soils were more acid, highly leached and poor in nutrients. Fertilizers (300 kg N and 456 kg K ha/year) and mulch of *Pennisetum purpureum* Schum. (80 Mg/ha/year) were applied, but no pesticides. Total yield potential for cooking banana, Giant French type plantain and Cavendish bananas are compared to the equivalent values calculated using data from the current experiment (Table 3.51).
Using the equation from Ortiz and Vuylsteke (1998) with data from the current experiment, our cultivars would appear to have consistently underperformed, even when current plant density was entered into the equation (Table 3.51). Bunch weights were only slightly lower in our experiment (data not shown) compared to those obtained by Ortiz and Vuylsteke (1998). Part of the explanation is due to different management practices (fertilizers and mulch) used in their experiment and also the plant density. Higher plant densities also result in more bunches per ha, but the weight of these bunches tends to be slightly less (Devos and Wilson, 1979). Also, no data were provided concerning pest pressure (weevils and/or nematodes) in the experiment by Ortiz and Vuylsteke (1998). So, pest pressure may have been considerably lower than in our experiment.

Table 3.51: Comparison of the total yield potential (Mg/ha/year) obtained by Ortiz and Vuylsteke (1998) with the equivalent values obtained using data from the current experiment.

Cultivar	Total yield potential Source: Ortiz and Vuylsteke (1998)*	Total yield potential (Hypothetical plant density of 1667 plants/ha)	Total yield potential (Real plant density of 2500 plants/ha)
Banane Cochon	29.2	13.2	19.8
Essong	32.8	19.3	28.9
Petite Naine	33.6	15.1	22.6

**: management practices: fertilizer application and mulching, data from several growth cycles (Ortiz and Vuylsteke, 1998).*

The equation of Ortiz and Vuylsteke also relies on the number of days to harvest. Air temperature has an important effect on growth and productivity of *Musa*. Depending on the cultivar, temperatures ranging from 20 to 30°C may result in quite similar productivity (Turner, 1995). However, optimal temperatures for dry matter production are in the lower 20's, whereas for the

[1] Yield potential = mean bunch weight x 365 x 1667 / (days to harvest x 1000; Ortiz and Vuylsteke, 1998).

rate of appearance of new leaves optimal temperatures are in the lower 30's (Turner, 1995). As stated above, leaf emission rates have a significant impact on the duration of growth cycles. Average daily temperature at Mbouroukou is 20°C, but closer to 30°C at Onne. Thus, the difference in temperature between the two sites explains the longer time to harvest at Mbouroukou and thus lower yields when expressed as Mg/ha/year.

The "total yield potential" (Ortiz and Vuylsteke, 1998) was lower than the calculated attainable yield in the current experiment (*i.e.* had each plant reached harvest and produced a bunch with weight equal to that of the heaviest bunch per cultivar). Even when plant densities were adjusted downwards to 1667 plants/ha, the attainable yield was still higher than the "total yield potential". The main advantage of using the attainable yield was that it allowed a calculation of the amount of yield loss attributable to reduced bunch weight. In this experiment, no effect of field history was seen on the relative yield loss due to reduced bunch weight.

3.5.6 Effect of cultivar on yield and dry matter accumulation

Essong produced heavier bunches but plants started flowering at least 3 months later and at least 20% fewer plants were harvested compared with the next slowest cultivar Banane Cochon. Ortiz and Vuylsteke (1998) state that tall plantain and banana cultivars tend to have a wider girth, slower growth cycle and flower later. So, some of this reduced production of Essong is simply cultivar-specific. Indeed, it is not surprising that the larger amount of biomass produced by Essong would take longer to assimilate.

More Essong plants were lost to premature death and toppling compared to the banana cultivars. At flowering, the highest nematode population densities were observed in the roots of Essong. Essong also suffered the highest disease severity and percentage of plants affected by the banana weevil. These results indicate that Essong was more vulnerable to adverse environmental conditions, such as planting in the dry season and pest pressure and confirm previous reports that, comparative to bananas, plantains are generally more susceptible to nematode attack (Price, 1994; Fogain and Gowen, 1998), weevil attack (Ortiz *et al.*, 1995; Pavis and Lemaire, 1996; Messiaen, 2002) and poor soil fertility (Wilson *et al.*, 1987; Swennen *et al.*, 1988).

Essong was the tallest cultivar, with the lowest pseudostem index, lowest number of functional roots and NDRI, and the highest RNI at flowering. The combination of tall plants with heavy bunches and a relatively smaller, more damaged root system amplifies it's susceptibility to toppling. Conversely, Banane Cochon and Petite Naine both had smaller bunches. Petite Naine

specifically was the shortest cultivar, had the highest pseudostem index, highest number of functional roots and NDRI, and the lowest RNI at flowering. No Petite Naine plants toppled. Banane Cochon rated intermediate between Essong and Petite Naine on these parameters and less Banane Cochon plants toppled compared to Essong.

When nematode population densities were examined at fixed time intervals, on the other hand, no cultivar-related differences were seen. At 1 YAP, a lower number of functional roots, and thus lower NDRI was seen for Essong (but no significant difference in RNI was observed between the cultivars). At 830 DAP no cultivar-related difference was seen in any of the root parameters observed. This would indicate that the increased susceptibility of Essong, compared to the two banana cultivars, is due to a combination of the smaller root system size and the longer duration of its growth cycle. This confirms a study carried out by Swennen *et al.* (1986), who found that the smaller root length of plantains, specifically the lower proportion of tertiary roots, could be a contributing factor to the lower productivity of plantains compared to bananas.

In the Canary Islands, where *P. goodeyi* is considered the most important nematode on export bananas, the cultivation of Dwarf Cavendish type AAA bananas, such as the cultivar Petite Naine, in combination with commercial management practices has greatly reduced toppling (Pinochet, 1998). Although Essong suffered relatively more plant losses during this experiment, the heavy bunches compensated for this lost production to some extent, resulting in a similar mean yield among the cultivars.

The objective of this experiment was to estimate the potential damage caused by high nematode pressure, so plants were not propped as a management strategy. Much loss can easily be prevented if propping is systematically implemented (Bridge, 1996), especially with tall, top-heavy cultivars such as Essong and Banane Cochon.

Due to apical dominance of the meristem in plantains, bananas generally have better suckering growth than plantains (Swennen, 1984; Ortiz and Vuylsteke, 1998), explaining the lower SGI on Essong (< 20%) compared to Banane Cochon (> 60%) and Petite Naine (> 50%). Bunch size for the plantain Essong was at least twice as large as bunch size for either banana cultivar. Swennen (1984) pointed out that the sink of a plantain bunch is so dominant that the relative dry matter of the sucker does not increase during the maturation period. Assuming suckers initiate at similar rates, the longer vegetative growth period of Essong explains the higher number of suckers produced by Essong at flowering. The number of suckers between cultivars was not significantly different when comparisons were made at specific time intervals, strengthening the assumption that sucker initiation, if not growth, was indeed similar among

the cultivars. No significant difference was seen in the vegetative growth index (VGI) per cultivar, although VGI was lower in the plantain Essong compared to the two banana cultivars Banane Cochon and Petite Naine.

So, although total assimilation did not differ much among the cultivars, indicated by the VGI and the number of suckers, the genetically determined sink competition within mats resulted in faster growth rates of the suckers on the banana cultivars, which may translate as earlier flowering and maturity in the ratoon crop (Tenkouano *et al.*, 2007). This is important because faster plant growth cycles result in higher overall productivity, especially when *Musa* yield is expressed as Mg/ha/year.

In the context of small-scale farming systems, the use of *Musa* cultivars with a shorter life cycle should be advocated in order to minimize yield loss. Such cultivars will tend to be smaller and have smaller bunches. The smaller bunch size will, however, be compensated by less toppling and a faster succession of harvests. Thus, a shorter growth cycle and not larger bunches should be the focus of breeding programmes for the improvement of small-scale farming systems.

3.5.7 Relationship between root necrosis and nematode population densities

In the current experiment, *P. goodeyi* was the main cause of root necrosis, compared with other nematode species found. Only for Banane Cochon did *R. similis* also contribute significantly to the root damage model, however, the association was weak. These results corroborate Bridge (1988) who identified *P. goodeyi* as the most important nematode responsible for severe root damage in the Kagera region, Tanzania.

Other reports in the literature where concomitant infections were studied are sometimes contradictory. Pattison *et al.* (2002) reported similar pathogenicity for *P. goodeyi* and *R. similis* in subtropical Australian banana plantations but pathogenicity of *R. similis* was less severe than that found in tropical (~ lower altitude) locations. Talwana *et al.* (2003) found higher damage caused by simultaneous infection with *R. similis* and *P. goodeyi* than with *P. goodeyi* alone.

Speijer and De Waele (2001), using multiple regression, found no contribution of *P. goodeyi* to RNI on East African Highland cooking bananas when concomitantly infected with *H. multicinctus*, *Meloidogyne* sp. and *R. similis*. On Pisang Awak (*Musa* group ABB), however, *P. goodeyi* was the best unique predictor, with *R. simlis* and *H. multicinctus* each contributing less to RNI, suggesting a cultivar-related response to nematode infection in the experiment (Speijer and De Waele, 2001).

Differing response to *P. goodeyi* may be related to the populations used. Much genetic variation, which may result in pathogenic variation, occurs between nematode populations (Roberts *et al.*, 1998; Young, 1998; De Waele 1996; Andrès *et al.*, 2001). Several studies have shown genetic and pathogenic variability of *R. similis* isolates collected from different geographical areas (Fogain & Gowen 1994, Hahn *et al.*, 1994; Hahn *et al.*, 1996; Fallas *et al.*, 1995; Fallas *et al.*, 1996; Elbadri *et al,* 2002). Likewise, inter- and intraspecific variation has been observed within the genus *Pratylenchus* (Andrès *et al.*, 2000; Waeyenberge *et al.*, 2000) and it has been suggested that genetic segregation within the species *P. goodeyi* may exist, as a Cameroonian population showed a completely different isozyme pattern in comparison to *P. goodeyi* populations from other regions (Andrès *et al.*, 2000).

Interactions with secondary pathogens, such as *Fusarium* spp. (Bridge *et al.*, 1997), may also aggravate relationships found between root necrosis and nematode infection levels, obscuring direct comparisons between differing experimental sites, especially where information of secondary pathogens is lacking.

3.5.8 Relationship between soil chemistry, nematode population densities, root damage, vegetative growth and productivity

The productivity of *Musa* plants depends strongly on the source/sink ratio (Jullien *et al,* 2001; Tenkouano *et al.*, 2007). Faster growing plants have higher leaf emission rates and thus higher leaf area (Swennen and De Langhe, 1985), allowing larger quantities of photoassimilates to be translocated to the bunch. It has also been suggested that the storage of carbohydrates in the form of starch in *Musa* corms (Sharrock, 1997) may reduce the importance of photosynthetic carbohydrate production by reallocating this carbon between individual organs (Tenkouano *et al.*, 2007). Needless to say, a healthy root system, sufficient soil nutrients and water availability are equally essential for vigorous plant growth and thus high yielding crops.

It was not possible in this experiment to delineate the effect of soil chemistry from that of nematode pressure using ANOVA procedures. However, by separating the database according to soil fertility using the results obtained through ANOVA, it was possible to mathematically remove the effect of soil chemistry from that of nematode pressure, allowing a comparison of the response of each cultivar to nematode pressure under differing levels of soil fertility, using regression procedures.

For all cultivars, models using data from the more fertile fields had a higher explanatory value than those derived from the less fertile field. Although, to

some extent, this may be due to a larger sample size, certain cultivar-related patterns were observed in the explanatory value of these models.

For the cultivar Petite Naine, models derived from data from more fertile soils were able to explain 4-37% of the variation in root parameters observed and *P. goodeyi* population densities were the main cause of damage in each model. Models derived from less fertile soils were unable to explain any variation.

For the cultivar Banane Cochon, between 29-42% of the variation in root parameters was explained using data from the more fertile soils. However, none of the variation in the number of dead roots could be explained using the current model. For all other root parameters in the more fertile field, *P. goodeyi* was the main cause of damage. In the less fertile soils, 16 and 29% of the variation in RNI and NDRI, respectively, was accounted for.

For the cultivar Essong, between 9-46% of the variation seen in root health could be explained using the models in the more fertile soils. For all parameters, *P. goodeyi* was the main cause of damage. In less fertile soils, 21 and 44% of the variation in NDRI and RNI, respectively, could be explained and again, *P. goodeyi* was the main cause of damage.

These results imply that for all cultivars, when soil fertility is relatively high, *P. goodeyi* is an important perpetrator of root damage and for Banane Cochon and Essong *P. goodeyi* is also an important cause of root damage in less fertile soils.

With regards to the models derived for bunch weight, the banana cultivars showed several similarities not found for the plantain cultivar, indicating that these may be related to the *Musa* AAA group. In less fertile soils, soil P content, root health and *P. goodeyi* population densities were unable to explain any variation observed in bunch weight of the banana cultivars. In more fertile soils, *P. goodeyi* population densities and root health explained between 17-37% of the variation observed in banana bunch weight.

These results corroborate the findings of McIntyre *et al.* (2000) who suggested that nematode damage only restricted the growth potential of bananas (*Musa* AAA cv. Mbwazirume) when soil fertility was sufficiently high, but that under poor soil fertility nematode damage was not a limiting factor.

In sharp contrast are the findings obtained for the plantain cultivar, Essong, especially in the less fertile soil. When root health parameters were used in the model, 58% of the variation in bunch weight was explained. Considering the impact of *P. goodeyi* on root health, these findings further underscore the importance of this nematode with regards to yield, specifically plantain yield under poor soil fertility. In the more fertile soils, *P. goodeyi* and root health did not contribute significantly to the models derived for bunch weight of the cultivar Essong, instead soil P content had the strongest influence on bunch weight.

Plantains are more susceptible to poor soil fertility and pest damage. A study similar to that done by McIntyre *et al.* (2000) in East Africa, but using the False Horn plantain cultivar Agbagba in Onne, Nigeria (Coyne *et al.*, 2005), found increased plant loss due to nematodes, with more root damage, toppling and premature death, especially when planted in poor soil conditions (i.e. non-mulched, in their experiment). Due to the cumulative effects of nematode damage to plantain in successive ratoons, Coyne *et al.* (2005) suggest that without inputs, including fertilizers and pesticides, plantains fail to produce enough in the ratoons to warrant management beyond the plant crop. Our findings corroborate these studies and further elucidate some of the mechanism leading to the increased vulnerability of plantains to adverse conditions.
In the East African Highlands, banana fields are often cultivated for many years without such severe yield loss as that witnessed for plantains. Our results also emphasize why plantains tend to thrive in home garden systems, where they benefit from the frequent input of kitchen waste and other household refuse. Under field conditions, where soil fertility does not always accommodate the stringent needs of plantains, shifting cultivation is more often observed (e.g. Swennen, 1984; Hauser, 2000).

The following generalizations are proposed:
For the plantain cultivar Essong:

1. Under low soil fertility, nematode control should be a major focus of attention in any comprehensive management scheme, including fertilizer application to reduce the susceptibility of the crop.
2. When soils are relatively more fertile, nematodes will pose less constraint for plantain production (although root health parameters will be affected) and yield improvements will be best achieved using a customized fertilization scheme, depending on a site-specific characterization of soil chemical properties prior to planting.

For the banana cultivars, Petite Naine and Banane Cochon:

1. Under low soil fertility, nematode control will have less impact on bunch weight. Therefore, improving soil fertility should be the main focus of management practices, through mulching (McIntyre *et al.*, 2000) and application of a customized fertilization scheme.
2. When soils are relatively more fertile, nematode control should be implemented as part of a comprehensive management scheme, including additional fertilization as required.

For practical purposes, however, both nematode control and adequate soil fertility management should be combined to obtain best results.

Chapter 4: Host status of twelve commonly cultivated crops of the Cameroon Highlands for the nematode *Pratylenchus goodeyi*[1]

The following chapter presents a study on the host status of 12 commonly cultivated crops of the Cameroon Highlands for *P. goodeyi*. Such information is useful for farmers who wish to expand an existing *Musa* plantation or who wish to establish a new *Musa* field on soil that was previously cultivated to a non-*Musa* crop, as it indicates which crop gives the highest likelihood of low initial nematode population densities. For the majority of small-scale farmers in the Cameroon Highlands who practice mixed cropping, such information can help to optimize the layout of their field.

4.1 Introduction

Deciding where to plant or expand an existing *Musa* spp. plantation has important implications with regard to nematode population buildup over time, especially when good productivity for several cycles is the goal.

Land that has been laid fallow for several years constitutes the best type of land for *Musa* cultivation, when fertility suffices. A minimum fallow duration of one year is advised to commercial banana plantations in southern lowland Cameroon, as a means to reduce weevil and *R. similis* population densities. In the densely populated Cameroon Highlands, fallowed land is not always available and if it is, old *Musa* mats may persist. Often, land previously cultivated with food crops is the only option.

Crop rotation constitutes the successive cultivation of crops or the alternation of cropping sequences in such a way that the buildup of nematode populations remains below the economic threshold level (Noe, 1998). This is done by limiting the available food source (= suitable host crop) for plant parasitic nematodes.

Similar to fallowing, crop rotation reduces population densities of the target pest, eventually resulting in lower infestation levels. However, whereas fallowing increases the biodiversity of soil biota (Cadet *et al.*, 2005) and

[1] The results of this chapter have been published: Jacobsen K., Maes, L., Norgrove, L., Mouassom, H., Hauser, S., De Waele, D. (2009). Host status of twelve commonly cultivated crops in the Cameroon Highlands for the nematode *Pratylenchus goodeyi*. International Journal of Pest Management 55 (4), 293-298.

improves soil quality (Hauser and Norgrove, 2001), crop rotation may allow pests to accumulate, due to the continued cultivation of the land with similar hosts. From the perspective of the farmer, however, the ability to use land continuously allows continued profit from the land, which may be a decisive factor for farmers when land is scarce.

The main objective of this study was to identify suitable non-host crops for the management of *P. goodeyi* within the context of *Musa* production in the Cameroon Highlands. Also, we aimed to elucidate the contradictions of previous host range studies of *P. goodeyi* (Price, 1994a; Mbwana *et al.*, 1995; Namaganda *et al.*, 2000) and determine the status of several other crops that are currently grown by farmers in the area.

4.2 Materials and methods

4.2.1 Site and experimental design

The experiment was carried out at Mbouroukou. For a detailed site description see Chapter 3.

An old banana field was cleared and 48 subplots (4.5 x 3.8 m) were prepared during July and August 2004. The infection level of *P. goodeyi* on the old banana plants was 8500 nematodes per 100 g fresh root weight (FRW). Other nematode species found in the roots of the old banana plants were *Meloidogyne* spp. (240 nematodes per 100 g FRW), *Helicotylenchus* spp. (17 nematodes per 100 g FRW) and *Hoplolaimus* spp. (5 nematodes per 100 g FRW).

Each subplot was planted to one of 12 crops at their normally recommended spacing: 1) *Allium cepa* (onion, local variety), 2) *Citrullus lanatus* (watermelon cv. Sugar baby), 3) *Colocasia esculenta* (taro, local variety), 4) *Abelmoschus esculentus* (okra, local variety), 5) *Ipomoea batatas* (sweet potato, cv. TIB1), 6) *Lycopersicon esculentum* (tomato, cv Roma), 7) *Musa* sp. (AAA group, cv. Grande Naine), 8) *Phaseolus vulgaris* (bean, local variety), 9) *Solanum tuberosum* (Irish potato, local variety); 10) *Xanthosoma sagittifolium* (cocoyam, local variety), 11) *Zea mays* (maize, cv. Kasaï), 12) *Zea mays* (maize, cv. CMS 8704). The banana cultivar, Grande Naine, a dessert banana, was included in the experiment as the susceptible reference crop. Nine tissue-culture propagated banana plants were planted per subplot (1.9 x 2.3 m).

The experiment was arranged in a completely randomized design with four replicates. Fertilizer was applied once at 3 months after planting according to local practices: 7 g NPK 12/14/19 per stand of beans (300 kg/ha), Irish potato (300 kg/ha), maize (100 kg/ha), okra (200 kg/ha), onion (235 kg/ha), sweet potato (145 kg/ha), tomato (250 kg/ha) and watermelon (100 kg/ha); 15g NPK 12/14/19 per stand of banana (100 kg/ha), cocoyam and taro (both 430 kg/ha).

Manual weeding was carried out when necessary. The crops were not harvested; instead, their use was to provide live roots for the duration of the experiment.

4.2.2 Nematode population density assessment

Sampling of roots and rhizosphere soil was carried out at 4 months after planting[1] when the population densities of *P. goodeyi* on the banana cultivar Grande Naine reached 9000 nematodes per 100 g FRW. Roots and rhizosphere soil were collected from randomly selected plants per subplot and grouped to form one bulk sample per subplot for roots and rhizosphere soil separately. The procedures used for extraction and identification of the nematode species are described in Chapter 2 (for root samples) and in Chapter 3 (for soil samples). Sometimes the quantity of roots from non-*Musa* plants was less than 50g; in this case, all roots were used for nematode extraction. Taxonomical verification was done in collaboration with the Nematology Unit, ARC-Plant Protection Research Institute, Queenswood, South Africa.

4.2.3 Statistical analysis

Pratylenchus goodeyi root population densities were expressed per 100 g FRW. The Levene's test showed heterogeneity of variances between groups (crops). Examination of the normal probability plots and the Kolmogorov-Smirnov test for normality revealed non-normality of the data. Log (x+1) transformation of the nematode population densities failed to normalize the data. When transformations are not successful in bringing the distributions of the error terms close enough to normality to meet the assumptions for Analysis of Variance (ANOVA), a nonparametric inference procedure can be useful (Kutner *et al.*, 2005). A Kruskal-Wallis analysis of ranks (nonparametric ANOVA equivalent) was used to examine the effect of treatment (crop) on the root population densities of *P. goodeyi*. A Mann-Whitney test (non-parametric *t*-test equivalent) was used to assist in the host status classification of the crops. Crops were classified as good hosts of *P. goodeyi* when their mean *P. goodeyi* root population density was not significantly different from the mean *P. goodeyi* root population density on banana, the susceptible reference crop. When their mean *P. goodeyi* root population density was significantly ($p \leq 0.05$) lower than the mean root population density on banana but higher than 1000 per 100 g FRW, the crops were classified as intermediate hosts. Crops with a mean *P. goodeyi* root population density significantly ($p \leq 0.05$) lower than the

[1] The reference population densitiy of 9000 *P. goodeyi* per 100g FRW was determined prior to the systematic sampling of the entire experiment, by examination of the roots of one plant in each subplot planted to banana. Roots and rhizosphere soil of all crops were thereafter sampled once a week, over a period of four weeks (at 15, 16, 17 and 18 weeks after planting). At each sampling date only one replica per crop was sampled.

mean root population density on banana and lower than 1000 nematodes per 100 g FRW were classified either as poor hosts (> 20 *P. goodeyi* per 100 g FRW) or very poor hosts (≤ 20 *P. goodeyi* per 100 g FRW).
All statistical analyses were done using SPSS for Windows, Student Version 14.0 (SPSS, Chicago, Illinois, USA) and SAS Enterprise Guide version 4.1 (SAS Institute Inc., Cary, NC, USA).

4.3 Results

Pratylenchus goodeyi population densities extracted from roots were significantly (χ^2 = 31.31; p≤0.001) different among the crops tested (Table 4.1). The mean population densities of *P. goodeyi* on bean and maize cv. CMS 8704 did not differ significantly from those on the susceptible reference crop, banana cv. Grande Naine. On maize cv. CMS 8704 and banana *P. goodeyi* was the dominant species (more than 50% of all plant parasitic nematodes extracted were *P. goodeyi*). *Pratylenchus goodeyi* was not the dominant plant parasitic nematode species on bean although the highest maximum *P. goodeyi* population density was found on this crop (31190 nematodes per 100 g FRW). Bean and maize cv. CMS 8704 can be classified as good hosts of *P. goodeyi*. The mean population densities of *P. goodeyi* on watermelon and onion were significantly (p≤0.05) lower than those on banana. However, their relatively high maximum *P. goodeyi* population densities (almost 9000 nematodes per 100 g FRW) show that these crops are capable of sustaining *P. goodeyi* populations. Watermelon and onion are therefore classified as intermediate hosts of *P. goodeyi*. The mean population densities of *P. goodeyi* on the other crops were also significantly (p≤0.05) lower than those on banana. Maize cv. Kasaï, taro, okra and Irish potato are only capable of supporting relatively small populations of *P. goodeyi* (on average 58-145 nematodes per 100 g FRW), and are classified as poor hosts of *P. goodeyi*. Both the mean and maximum population densities of *P. goodeyi* on cocoyam, tomato and sweet potato were very low (≤ 20 and ≤ 100 nematodes per 100 g FRW, respectively). These crops are therefore classified as very poor hosts of *P. goodeyi*. *Pratylenchus goodeyi* was extracted from the roots of all crops but was not found in the rhizosphere soil of onion, maize cv. Kasaï, Irish potato and tomato.
In addition to *P. goodeyi*, species belonging to seven plant parasitic nematode genera were also found associated with the crops included in the experiment (Table 4.2). *Meloidogyne* spp. and *Helicotylenchus* spp. were extracted from both the roots and the rhizosphere soil of all crops. *Scutellonema* spp. Andrássy, 1958 were extracted from the roots of all crops but were not found in the rhizosphere soil of okra. *Helicotylenchus* spp. were the most common nematode species found in the roots of bean, Irish potato, maize cv. Kasaï,

tomato and onion. *Meloidogyne* spp. in the roots of cocoyam and okra; *Scutellonema* spp. in the roots of sweet potato and taro. *Mesocriconema* spp. Andrássy, 1965 were only extracted from the roots of bean, but were found in the rhizosphere soil of banana, bean, Irish potato, both maize cultivars, okra, sweet potato and tomato. Trace numbers of *Aphelenchoides* spp. Fischer, 1984 (extracted from the roots of onion and maize cv. CMS 8704), *Psilenchus* spp. de Man, 1921 (extracted from the roots of bean) and *Pratylenchus coffeae* (extracted from the roots of taro) were also found.

Table 4.1: Evaluation of the host status of 12 crops for *Pratylenchus goodeyi*: mean and maximum densities of *P. goodeyi* per 100 g fresh root weight and percentage *P. goodeyi* in comparison to other plant parasitic nematodes.

Crop[§]	n[†]	Mean *P. goodeyi* population density[‡]	Maximum *P. goodeyi* population density[‡]	% *P. goodeyi* of nematodes extracted	Pair-wise comparison with reference host crop (p-level)[θ]		Host status
					means	% *P. goodeyi*	
Banana cv. Grande Naine	4	12787	17500	86.83	-	-	Host
Beans	4	11883	31190	35.87	0.56	0.02	Host
Maize cv. CMS'8704	4	7523	15227	89.04	0.15	0.56	Host
Watermelon cv. Sugar baby	4	2991	8789	43.57	0.02	0.25	Intermediate host
Onion	4	2474	8800	33.26	0.02	0.02	Intermediate host
Maize cv. Kasai	4	308	567	26.10	0.02	0.02	Poor host
Taro	4	145	300	7.53	0.02	0.02	Poor host
Okra	4	92	238	3.77	0.02	0.02	Poor host
Irish potato	4	58	200	1.18	0.02	0.02	Poor host
Sweet potato cv. TIB1	4	20	79	0.70	0.02	0.02	Very poor host
Cocoyam	4	8	33	1.32	0.02	0.02	Very poor host
Tomato cv. Roma	4	8	33	1.09	0.02	0.02	Very poor host
Significance[∞]		$p<0.001$; $\chi^2=31.31$		$p<0.001$; $\chi^2=31.32$			

§: local variety unless otherwise stated; †: n represents number of replicates for each crop; ‡: Number of P. goodeyi per 100 g fresh root weight; ∞: Kruskal Wallis analysis of ranks; θ: Mann-Whitney test.

Table 4.2: Nematode species composition and population densities per crop in order of abundance in the roots and rhizosphere soil.

Crop	Nematode spp. in roots	Mean nematode population density / 100 g FRW	Nematode spp. in soil	Mean nematode population density / 250 ml soil
Banana	*Pratylenchus goodeyi*	12787	*Helicotylenchus dihystera*	183
	Helicotylenchus spp.	716	*Meloidogyne* spp.	170
	Meloidogyne spp.	507	*Pratylenchus goodeyi*	37
	Scutellonema spp.	397	*Scutellonema* spp.	21
			Mesocriconema sphaerocephalum	8
Beans	*Helicotylenchus dihystera*	25682	*Mesocriconema* spp.	913
	Meloidogyne spp.	17365	*Helicotylenchus dihystera*	328
	Pratylenchus goodeyi	11883	*Pratylenchus goodeyi*	254
	Scutellonema spp. *S. clathricaudatum*	1450	*Scutellonema* spp.	207
	Mesocriconema spp.	42	*Meloidogyne* spp.	50
	Ditylenchus spp. Filipjev, 1936	nd		
	Psilenchus spp.	nd		
Cocoyam	*Meloidogyne* spp.	1210	*Helicotylenchus* spp.	263
	Helicotylenchus spp.	64	*Meloidogyne* spp.	25
	Scutellonema spp.	25	*Pratylenchus goodeyi*	17
	Pratylenchus goodeyi	8	*Scutellonema* spp.	4
Irish potato	*Helicotylenchus* spp.	2484	*Scutellonema* spp.	167
	Meloidogyne spp.	494	*Meloidogyne* spp.	53
	Scutellonema spp.	191	*Helicotylenchus* spp. *H. dihystera*	21
	Pratylenchus goodeyi	58	*Mesocriconema* spp.	4
Maize cv CMS 8704	*Pratylenchus goodeyi*	7523	*Helicotylenchus* spp. *H. dihystera*	167
	Helicotylenchus spp. *H. dihystera*	450	*Meloidogyne* spp.	77
	Meloidogyne spp.	132	*Scutellonema* spp.	43
	Scutellonema spp.	50	*Mesocriconema* spp.	14
	Aphelenchoides spp.	nd	*Pratylenchus goodeyi*	13
Maize cv Kasaï	*Helicotylenchus* spp. *H. dihystera*	1064	*Helicotylenchus* spp. *H. dihystera*	817
	Pratylenchus goodeyi	308	*Mesocriconema sphaerocephalum*	513
	Scutellonema spp.	231	*Scutellonema cavenessi* Sher, 1964	46
	Meloidogyne spp.	100	*Meloidogyne* spp.	33

Table 4.2 continued

Okra	*Meloidogyne* spp.	15976	*Helicotylenchus* spp. *H. dihystera*	167
	Helicotylenchus spp. *H. dihystera*	3822	*Meloidogyne* spp.	21
	Scutellonema clathricaudatum	764	*Pratylenchus goodeyi*	8
	Pratylenchus goodeyi	92	*Mesocriconema sphaerocephalum*	4
Onion	*Helicotylenchus* spp.	3345	*Helicotylenchus dihystera*	1317
	Pratylenchus goodeyi	2474	*Scutellonema* spp.	192
	Scutellonema spp. *S. bradys* Steiner & LeHew, 1933) Andrassy, 1958 *S. clathricaudatum* Whitehead, 1960	1864	*Meloidogyne* spp.	13
	Meloidogyne spp.	232		
	Aphelenchoides spp.	nd		
Sweet potato	*Scutellonema* spp. *S. bradys* *S. clathricaudatum*	2040	*Helicotylenchus* spp. *H. dihystera*	358
	Helicotylenchus spp.	1487	*Scutellonema cavenessi*	54
	Meloidogyne spp.	227	*Mesocriconema* spp.	21
	Pratylenchus goodeyi	20	*Pratylenchus goodeyi*	4
			Meloidogyne spp.	4
Taro	*Scutellonema* spp. *S. clathricaudatum*	3563	*Scutellonema* spp. *S. clathricaudatum*	54
	Meloidogyne spp.	2728	*Meloidogyne* spp.	29
	Helicotylenchus spp.	1777	*Mesocriconema* spp.	29
	Pratylenchus goodeyi	145	*Helicotylenchus* spp.	21
	Pratylenchus coffeae	nd	*Pratylenchus goodeyi*	4
Tomato	*Helicotylenchus* spp.	4156	*Helicotylenchus* spp. *H. dihystera*	375
	Meloidogyne spp.	1233	*Mesocriconema sphaerocephalum*	49
	Scutellonema spp.	205	*Scutellonema cavenessi*	42
	Pratylenchus goodeyi	8	*Meloidogyne* spp.	25
Watermelon	*Pratylenchus goodeyi*	2991	*Helicotylenchus* spp. *H. dihystera*	413
	Helicotylenchus dihystera	995	*Scutellonema* spp.	42
	Meloidogyne spp.	621	*Meloidogyne* spp.	8
	Scutellonema spp.	568	*Pratylenchus goodeyi*	4

Legend: FRW: fresh root weight; nd: nematode species present but exact nematode population density of this species not determined; Genera that could not be identified to species level are designated as 'spp.'

4.4 Discussion

A total of 123 plant species have been screened so far for their host status for *P. goodeyi* (Price, 1994a; Mbwana *et al.*, 1995; Prasad *et al.*, 1995; Namaganda *et al.*, 2000; our study). Only about 10% of these plant species were classified as good hosts of *P. goodeyi* by one or more authors: four food crops (banana, plantain, onion and watermelon), one medicinal crop (*Plectranthus barbatus* Andr.), one fodder crop (*Tripsacum laxam* Nash.) and six weeds *(Cynodon* sp., Rich., *Cyperus esculentus* L., *Hyparrhenia rufa* (Nees) Stapf., *Leonotis mollissima* (Pers.) R.Br., *Solanum incanum* L. and *Tridax* sp.). Therefore, our study reflects previous reports (Price, 1994a; Mbwana *et al.*, 1995; Namaganda *et al.*, 2000) that *P. goodeyi* has a relatively narrow host range, especially in comparison to other *Pratylenchus* spp.

However, we also concur with the cautionary remarks made by Prasad *et al.* (1995) that the host range of *P. goodeyi* is wider than previously thought. Another 10% of the 123 plant species screened, received the ambiguous classification of good host in one study and very poor host or non-host of *P. goodeyi* in another study (Table 4.3): eight food crops (cassava, okra, taro, bean, tomato, Irish potato, sorghum and maize), one agroforestry crop (*Leucana leucocephala* (Lam.) De Witt) and four weeds (*Bidens pilosa, Commelina benghalensis* L., *Digitaria scalarum* (Schweinf.) Chiov. and *Solanum nigrum*).

The contradictions between the five studies (Table 4.3) suggest that the classification of plants as non-hosts or very poor hosts should be considered carefully before advising these as rotation crops to farmers.

The classification of a plant species as a host for a plant parasitic nematode may vary depending on a combination of factors. Firstly, the use of crops obtained locally without reference to cultivar confuses the interpretation of the results between the five studies, as was underlined in the current study by the variable susceptibility of the maize cultivars. Also, the *Musa* cultivars used as a reference in the five host range studies were not identical[1]. Considering that the *P. goodeyi* root population density on the reference *Musa* cultivar in each of the studies was used as a measure for host suitability, it is possible that the use of a more susceptible cultivar could lead to the classification of relatively more plants as (very) poor hosts. No reports on the comparative susceptibility of the

[1] The reference cultivars used in each study were: 'French Sombre' (*Musa* AAB, plantain subgroup type French Medium) (Price, 1994a), 'Nyoya' (*Musa* AAA, East African highland banana subgroup) (Mbwana *et al.*, 1995), 'Nabusa' (*Musa* AAA, East African highland banana subgroup) (Namaganda *et al.*, 2000) and 'Grande Naine' (*Musa* AAA Cavendish subgroup) (our study). In the study by Prasad *et al.* (1995) no reference cultivar was used.

Musa cultivars used in these five studies could be found in the literature. Similarly, the type of *Musa* planting material used (suckers or *in vitro* plantlets) can impact the number of *P. goodeyi* recovered at sampling, thus impacting conclusions of host suitability of the test crops.

Table 4.3: Cultivar-related differences in host status of plant species for *Pratylenchus goodeyi.*

Botanical (common) name	Cultivar (study; see legend below)			
	(Intermediate) host	Poor host	Very poor host	Immune
Abelmoschus esculentus (okra)		Local cultivar (1/5)		Local cultivar (2)
Bidens pilosa (weed)	Local variey (3)			Local variety (2/4)
Colocasia esculenta (taro)		Local cultivar (1/5)		Local cultivar (2)
Commelina benghalensis (weed)	Local variety (2/3)		Local variety (4)	
Digitaria scalarum (weed)	Local variety (3)			Local variety (2/4*)
Leucana leucocephala (white lead tree)	Local variety (3)			Local variety (2)
Lycopersicon esculentum (tomato)	cv. Money maker (3)		cv. Roma (5)	Local cultivar (2)
Manihot esculenta (cassava)		cv. 8017 (1)		Local cultivar (2) , cv. Bukalasa 11 (4)
Phaseolus vulgaris (beans)	Local cultivar (1/5)	cv. Kawanda 20 (4)		Local cultivar (2)
Solanum nigrum (weed)	Local variety (3)			Local variety (4*)
Solanum tuberosum (Irish potato)	cv. Annette (3)	Local cultivar (5)		Local cultivar (1/2)
Sorghum bicolor (sorghum)	cv. Hybrid 6 (3)			ssp. bicolor (syn. *S. vulgare*) (2)
Zea mays (maize)	cv. CMS 850 (1), cv. Hybrid 512 (3), cv. CMS 8704 (5)	cv. Kawanda Composite A (4), cv. Kasaï (5)		cv. EH 85109 (2)

(1): Price (1994a); Location: Ekona, Cameroon (120 km from our study on similar soils); Set-up: field trial; (2): Mbwana et al. (1995); Location: Maruku, Tanzania; Set-up: field trial; (3): Prasad et al. (1995); Location: Oyugis, Kenya; Set-up: sampling of existing plants in a Musa *plantation infested with* P. goodeyi*; (4): Namaganda et al. (2000); Location: Kawanda, Uganda; Set-up: pot experiment; 4*: Namaganda et al. (2000); Location: Bushenyi and Kawanda, Uganda; Set-up: sampling of existing plants in a* Musa *plantation infested with* P. goodeyi*; (5): Our study; Location: Mbouroukou, Cameroon; Set-up: field trial.*

Secondly, differences in pathogenicity among nematode populations can be expected, considering the different locations where the studies were carried out. Intraspecific variation has been shown for isolates of *P. goodeyi* originating from different locations (Andrès *et al.*, 2000).

Finally, methodological differences in the experimental protocol used, may have contributed to the contradictions observed. In addition to the differences cited above, the protocols differed in: the criteria used to define host suitability, the experimental set-up, the time of sampling and the extraction methods.

The use of different criteria to define host status may have confused interpretations concerning the degree of host suitability. In the study by Mbwana *et al.* (1995), the difference in means between treatments were analysed using ANOVA. However, both Mbwana *et al.* (1995) and Prasad *et al.* (1996) made no further distinction in the degree of host suitability, classifying plants as host if *P. goodeyi* was extracted, regardless of the quantity found. The studies by Price (1994a), Namaganda *et al.* (2000) and our study, on the other hand, reported differing degrees of host suitability depending on the quantity of *P. goodeyi* extracted. When standardized inoculums were used as a source of infection (Namaganda *et al.*, 2000), the 'reproductive rating' (R = *P. goodeyi* population density on the test plant / *P. goodeyi* population density on the *Musa* cultivar; Tedford and Fortnum, 1988) was used to determine the degree of host suitability. In the field study by Price (1994a) and our study, the degree of host suitability was determined by analysing the difference in means between treatments and considering the quantity of *P. goodeyi* extracted from the roots[1].

The singular distinction into host or non-host, based on the presence or absence of *P. goodeyi* (Mbwana *et al.*, 1995; Prasad, *et al.*, 1996) obscures the potential of very poor hosts as possible rotation crops: several plant species classified as non-hosts (or immune) by Price (1994a) and Mbwana *et al.* (1995) were consequently identified as very poor hosts by Namaganda *et al.* (2000) and our study. Therefore, a distinction concerning the degree of host suitability is useful.

Any factor in the experimental protocol that impacts the number of *P. goodeyi* recovered from the test plants, can impact the interpretation of results concerning host status. Thus, the different experimental set-ups used in the five studies may have contributed to the contradictions found. For example, the method of inoculation and the inoculation level differed in each of the studies:

[1] In the study of Namaganda *et al.* (2000) the degree of host suitability was defined as follows: for R > 0.5 plants were considered host of *P. goodeyi* and for R < 0.5 plants were considered poor host. The criteria used to determine the degree of host suitability in our study are given in the materials section; the criteria are not explicity reported in Price (1994a).

in the study by Namaganda *et al.* (2000), a known inoculum (500-1200 *P. goodeyi* per pot) was used as an infection source[1]; in the other studies (Price, 1994a; Prasad *et al.*, 1995; Mbwana *et al.*, 1996; our study), the plant species under investigation grew in fields where *Musa* infested with *P. goodeyi*[2] (between 8500 – 20000 *P. goodeyi* per 100g FRW) was cultivated. The final nematode population density (*Pf*) obtained on a test plant will, however, relate to the initial population density (*Pi*) present in the soil before planting (Seinhorst, 1967). So, a low *Pi* may lead to relatively more plants classified as (very) poor hosts.

Additionally, under field conditions nematodes have a patchy distribution (Barker *et al.*, 1998). So, reporting only the mean nematode population density is valid only when standardized inoculums are used, as in the study carried out by Namaganda *et al.* (2000). When studies are conducted in the field, on the other hand, the maximum nematode population density should also be reported as it can provide valuable information about the capacity of the nematode to reproduce on the plant species under investigation. In our study, for example, the highest mean density was found on banana. The highest maximum density was, however, found on beans.

The number of *P. goodeyi* recovered at sampling also depends on the duration of its lifecycle, which is species-dependent (Van Coppenolle *et al.*, 1999; Gems, 2000). Prasad *et al.* (1999) recorded 24-30 days for the lifecycle of *P. goodeyi* in banana roots, depending on host suitability. The interval between inoculation and evaluation in the trial carried out by Namaganda *et al.* (2000) was eight weeks (56 days), allowing for the completion of approximately two life cycles of *P. goodeyi* in the test plants. Price (1994a) and our study used an interval time of four months (equivalent to approximately four life cycles). Mbwana *et al.* (1995) evaluated their experiments at two intervals (60 and 360 days after planting; the results of Mbwana *et al.*, 1996 in Table 5.3 reflect data obtained at 360 days after planting). The study by Prasad *et al.* (1995) was carried out on plants growing in an infested banana field, but the duration that these plants had been growing there was not specified.

[1]Initially 500 *P. goodeyi* were inoculated per pot, but in a second experiment the inoculum was raised to 1200 in order to increase the root penetration of *P. goodeyi*; in both experiments chopped root pieces were used (Namaganda *et al.*, 2000).

[2] The infestation level in the field studies was determined by examining the roots of old *Musa* spp. in the field where the experiment would be planted. The mean population density of *P. goodeyi* per 100 g FRW equalled 8500, 15000 and 20000 in the fields used in our study, the study of Price (1994a) and the study of Prasad *et al.* (1995), respectively. The number of *P. goodeyi* found in the roots of the old *Musa* spp. in the study of Mbwana *et al.* (1996) was not reported.

Extraction methods for plant parasitic nematodes from soil and root samples are known to differ in their efficiency (Viglierchio and Schmitt, 1983a; Viglierchio and Schmitt, 1983b; Viglierchio and Yamashita, 1983; Hooper, 1990). For example, maceration and sieving recovers a greater number of nematodes than maceration and incubation (Quimi and Villacis, 1977; Hooper, 1990). McSorley *et al.* (1984) found mist chamber extraction among the best methods for extracting *Pratylenchus* spp., but maceration and sieving was comparable in efficiency and suitable for most other nematode species common to *Musa*. Differences in extraction methodology between the host range studies may also have contributed to the variable host status of plants, especially with regards to plants classified as non-hosts or 'poor' hosts.

Additionally, environmental conditions (Noe, 1991; Kimpinski & Sturtz, 2003; Yeon *et al.*, 2003) and the growth stage of the plant at sampling (Barker & Olthof, 1976) will add to the variability in *Pf* found in the roots of a test plant, making it exceedingly difficult to compare the results obtained from several host range studies, which differ in one or several variables.

While some factors cannot be controlled, the use of a more uniform protocol could improve the validity of the results and increase their applicability. Suggestions to improve the methodology of host range studies for nematodes affecting *Musa* spp. are given in the text box, below.

Plant parasitic nematodes often occur in multiple species communities and efforts to control *P. goodeyi* may enhance population densities of other nematode species (Table 4.2; Desaeger and Rao, 2000; Luc *et al.*, 2005). Table 4.4 gives an overview of plants that were identified in at least two studies as non-host or very poor host for *P. goodeyi* (excluding contradictory reports).

Table 4.4: Summary of plant species identified as very poor hosts and non-hosts for *Pratylenchus goodeyi* in at least two host range studies.

Botanical (common) name	Cultivar	
	Very poor host	Non-host
Ageratum conyzoides (weed)		Local variety (2/4)
Arachis hypogaea (groundnut)	Local cultivar (1)	Local cultivar (2)
		cv. Red Beauty (3)
Xanthosoma sagittifolium (cocoyam)	Local cultivar (1/4)	
Ipomoea batatas (sweet potato)	cv. New Kawongo (3)	Local cultivar (2)
	cv. TIB1 (4)	cv. TIB1 (1)

1: Price (1994a); Location: Ekona, Cameroon (120 km from our study on similar soils); 2: Mbwana et al. (1995); Location: Maruku, Tanzania; 3: Namaganda et al. (2000); Location: Kawanda, Uganda; 4: Our study; Location: Mbouroukou, Cameroon;

Suggested methodology for host range studies of nematodes affecting *Musa* spp.

- Only known cultivars should be used and their names should always be reported. When testing for the same nematode species, the same susceptible *Musa* cultivar should be used as a reference crop and the type of planting material (*in-vitro* or sucker) should be reported.
- Both a pot study and a field study should be carried out, whereby the results obtained in the pot study should be verified in the field study.
    - Further research should determine the optimal duration of the host range studies in pots and in the field.
- The initial inoculum level should be reported: for pot studies, a known inoculum should be used and reported; for field studies, the inoculum level present in the roots of a susceptible *Musa* sp. growing in the field prior to planting the experiment should be evaluated and reported.
    - Further research should determine the optimal: method of inoculation (using infected root pieces or extracted female nematodes); time of inoculation after planting and the inoculation level.
- For field studies, the *Musa* sp. growing in the field prior to planting the experiment should be uprooted, chopped into smaller pieces and left to rot in the field.
- For field studies, in order to optimize the homogeneity of variances, thus allowing ANOVA as an analysis method, the number of plots should have precedence over the size of the plots. A balance between available time and resources is necessary, however.
- For field studies, both the mean and maximum nematode root population densities should be reported.
- Maceration and sieving or mist chamber extraction are the preferred extraction methods.
- The degree of host suitability should be determined: for pot studies, the reproduction factor should be used; for field studies, the criteria detailed in our study can be used.

The trace numbers of *P. goodeyi* recorded on sweet potato in our study agree with Namaganda *et al.* (2000) that this crop is not immune, as was reported by

Price (1994a) and Mbwana *et al.* (1995), but rather a very poor host for *P. goodeyi*. The weed *Ageratum conyzoides,* and the crops groundnut, cocoyam and sweet potato were identified as non-hosts or as very poor hosts for *P. goodeyi* (Price, 1994a; Mbwana *et al.*, 1995; Prasad *et al.*, 1995; Namaganda *et al.*, 2000; our study) indicating that they could be suitable rotation crops if care is taken to use the cultivars specified in Table 4.4. Local varieties should always be screened before advising these as rotation crops for reducing *P. goodeyi*.

Farmers in the Cameroon Highlands plant mainly in mixed cropping systems (Jacobsen *et al.*, 2004). The ecological stability of these systems stems from the diversity of crops and cultivars used, which reduces the risks of pest accumulation inherent to long-term cultivation (Bridge, 1996; Knops *et al.*, 1999).

When *Musa* production is market-oriented, crop rotation is often implemented as a component of an integrated pest management plan, whereby fields are alternated between host and non-host crop in an effort to reduce nematode damage. In commercial banana plantations involving large monocropped fields, crop rotation is straightforward. In the context of mixed cropping, on the other hand, crop rotation in the traditional sense would require some streamlining in order to be effective.

Two adaptations can be envisaged. In a first adaptation, the farmer could remove all host crops on a plot of land for a period of time, long enough to reduce nematode population densities below the damage threshold. Only after this period would the host crops be cultivated again on this plot of land. The main problem with this adaptation is that it assumes that farmers either have sufficient land to plant the host crops elsewhere or that certain host crops are not that important for the family. In the case of *Musa* cultivation in the densely populated Cameroon Highlands, both land constraints and the importance of *Musa* spp. for farming families make the implementation of this first adaptation less likely. In a second adaptation, the farmer could remove the host crop from one area of a plot of land and replant this crop into another area where a non-host crop was grown. Thus practising crop rotation on a smaller scale, by alternating small areas of host and non-host crops within the same plot of land. The main issue with the second adaptation is finding a method that will reduce the re-infestation of nematode-free areas.

In a study carried out by Duncan *et al.* (1990), a barrier method was used in citrus orchards to reduce the spread of *Radopholus citrophilus*[1] from infected

[1] *Radopholus citrophilus* Huettel, Dickson and Kaplan, 1984 syn. *R. similis*, citrus race (Loof, 1991)

to non-infected seedlings. They found that *R. citrophilus* was unable to migrate in root-free soil. When host roots were permitted to grow towards one another, conversely, the nematode moved >1.4m in one year from infected to uninfected seedlings. By pruning the roots of host plants, they were able to greatly restrict inter-orchard spread of the nematode (Duncan *et al.*, 1990). Thus, it appears that it is possible to delimit, to some extent, the area of infestation within a field.

Considering the migratory capacity of a nematode species, it should thus be possible to practice crop rotation within a mixed cropping system by changing the layout of the field. In the case of *Musa*-based cropping systems in the Cameroon Highlands, the size of the area would need to be larger than the area of soil occupied by the roots of the *Musa* plant (or the roots would have to be pruned). Planting a non-host barrier crop around the *Musa* plant may further minimize re-infestation and prolong the duration of reduced infection levels. Nematode infection through run-off after heavy rains might still be expected, but nematode population build-up over time would most likely be reduced. Further research should determine the optimal size of such an area.

Another promising solution to pest-related yield loss is the use of resistant cultivars (Dochez *et al.*, 2004). Additional screening of *Musa* cultivars for *P. goodeyi* resistance or tolerance is needed, as the cultivation of such cultivars in combination with poor host crops could further increase the productive potential of the land.

Chapter 5: Conclusions and perspectives

The survey results (Chapter 2) demonstrated the growing importance of local food crop production for small-scale farming households in the Cameroon Highlands. Among the 38 food crops cultivated, *Musa* spp. were cited as the most important by a majority of farmers, especially in comparison to the traditional cash crop, coffee. The specific importance of *Musa* spp. can be explained by their cultural significance, as well as the food security and cash income they provide.

Despite the importance given to *Musa* spp., farmers were only vaguely aware of pests and diseases affecting *Musa* spp. and this awareness was based mostly on empirical evidence. Only 15% of the 216 farmers interviewed in the Cameroon Highlands had ever heard of a nematode before or were aware of damage caused by them. Such a lack of awareness can easily trigger widespread damage, as infected planting material is unknowingly spread from field to field and from farm to farm.

Pratylenchus goodeyi was the most abundant and frequently found nematode species of *Musa* fields in the Cameroon Highlands. In the field study (Chapter 3), *P. goodeyi* was identified as the main perpetrator of root necrosis among the nematode species found, responsible for toppling, lengthening of the growth cycle and reduced bunch weight. Thus, *P. goodeyi* can be regarded as a serious constraint for *Musa* production in the Cameroon Highlands.

Pratylenchus goodeyi is able to survive on native African plant species and is most likely indigenous to African highland regions. However, in the absence of a preferred host, population densities remain relatively low. Therefore, when fallowing is used as a method to reduce population densities of *P. goodeyi,* it is imperative that all preferred hosts are eliminated for the period of time that a field is kept fallow.

In a *Musa* field that had been abandoned for 14 years (Chapter 3), we demonstrated that the severity of infection in a new *Musa* plantation is directly related to the number of *Musa* mats that remain in the field during the fallow period. The yield obtained from the area of the field where no *Musa* had been growing prior to set-up of the experiment was 212% higher than from the area of the field where many *Musa* mats had been growing.

Nematode related damage, such as toppling was 8-15 times higher in the area of the field where *Musa* plants had grown compared to the *Musa*-free area. Nematode related root damage was also proportionate to the duration of exposure, such that the cultivar with the longest growth cycle (Essong) suffered more. In the context of small-scale farming systems, the use of *Musa* cultivars with a shorter life cycle should be advocated in order to minimize yield loss.

Such cultivars will tend to be smaller and have smaller bunches. The smaller bunch size will, however, be compensated by less toppling and a faster succession of harvests. Thus, a shorter growth cycle and not larger bunches should be the focus of breeding programmes for the improvement of small-scale farming systems. For larger, top-heavy cultivars, propping upon flowering is mandatory in order to avoid toppling.

An important interaction was seen between soil fertility and *P. goodeyi* infection, highlighting the vulnerability of plantains to adverse conditions. An increased susceptibility of plantains to nematode-related root damage can be expected when soil fertility is compromised. The banana cultivars, on the other hand, showed a less vulnerable reaction to the combined effects of low soil fertility and nematode pressure. These cultivar-related differences in response to soil fertility and nematode damage, explain why banana fields in East Africa are often cultivated for several decennia, whereas plantain fields in Central and West Africa are more often part of a shifting cultivation. Conversely, in home gardens, plantains are known to flourish due to the frequent application of kitchen waste and other inputs.

Clearly both plantains and bananas will benefit from improved soil fertility and low nematode pressure. While customized fertilization schemes may fall outside the family budget of many small-scale farming households, the use of nematode-free planting materials is a relatively easy and low-cost measure. More importantly, the synergy between nematode pressure and low soil fertility indicates that the potential of fertilizer application may be wasted if nematode control measures are not simultaneously implemented.

In the densely populated Cameroon Highlands, land constraints are often a problem and finding enough land that has been left to fallow without any cultivation for a sufficiently long period may not be possible. Therefore, selecting land that has been planted to a poor host for *P. goodeyi* may be an alternative to fallowed land when expanding or planting a new *Musa* field. In the host range study (Chapter 4), some of the most commonly cultivated crops in the Cameroon Highlands were examined regarding their host suitability for *P. goodeyi*. Beans and maize (cv. CMS 8704) were identified as good hosts; watermelon and onion were intermediate hosts; maize (cv. Kasaï), taro, okra, Irish potato and sweet potato were poor hosts, while cocoyam and tomato were very poor hosts. The preferred hosts for *P. goodeyi* are thus *Musa* spp., beans and maize (although not all cultivars are equally susceptible).

When our results were compared with those obtained in other host range studies, several discrepancies were observed, leading to the conclusion that a more uniform protocol could improve the results of host range studies of *Musa* nematodes. A list of proposed improvements is given in Chapter 4. Additional

research should determine the optimal duration of the host range studies, the optimal inoculation level and inoculation time after planting and the optimal method of inoculation.

Mixed cropping systems are the norm for most small-scale farmers in sub-Saharan Africa. However, the use of rotation crops to reduce nematode population densities is most often implemented with mono-cropping systems in mind. It was suggested that crop rotation on a smaller scale, *i.e.* the alternation of host and non-host crop areas within the same field, might facilitate the use of this control option by small-scale farmers. Further research is needed to test the applicability of crop rotation within mixed cropping systems.

The benefits of using clean planting material have been illustrated by numerous studies. However, as the results from the experiment in Chapter 3 clearly demonstrated, clean planting material is almost useless when planted into fields that are infested with *P. goodeyi* (although the results may have been even more drastic if already infested materials were used). Additional inputs, such as fertilizers and mulch, and management practices, such as propping, could undoubtedly have prevented much of this loss. On the other hand, planting clean materials into almost any sufficiently fertile field in the Cameroon Highlands where no beans, maize or *Musa* were previously grown may be enough to achieve a good harvest for at least two cycles with very minor input or management effort whatsoever (barring the presence of other infections, such as weevils).

The importance of *Musa* spp. for farming households, the low levels of pest awareness and the capacity of *P. goodeyi* to cause severe yield loss, underscore a clear and urgent need for increased farmer training initiatives. These initiatives should focus on integrated pest management (IPM) for *Musa* spp. Some IPM strategies that might be particularly successful in the Cameroon Highlands include the following: (1) rotation of *Musa* spp. with crops that are poor hosts for *P. goodeyi*; (2) propping at flowering to prevent toppling; (3) use of fertilizer, manure and/or mulch to improve soil fertility and reduce the duration of the growth cycle; (4) use of clean planting materials, such as pared and heat-treated suckers; and (5) use of cultivars with a high tolerance to adverse conditions, including nematode infestation.

The survey of farming households was carried out in close collaboration with the national extension service (NAERP). This enabled us to discuss issues directly with farmers in their own language, through a contact person familiar to the farmers. This successful collaboration suggests that regular contact between *Musa* researchers and the NAERP could be beneficial for farmers.

Such contact would ease the transfer of existing and new pest management technologies to farmers without requiring large amounts of time, money or manpower. The high level of literacy in Cameroon, especially in comparison with neighbouring countries, means that farmer training pamphlets might be another cost effective option for reaching farmers in otherwise difficult to reach locations. The willingness of farmers to participate in future training programs should not be overlooked: an increase in the number of training initiatives would no doubt boost *Musa* productivity in the region, which given the marketability of this crop, can lead to an improvement in the livelihoods of farming households.

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Annex 1: On farm interviews

The following interview was used during the survey of farming practices of the Cameroon Highlands[1]. The layout has been adapted to the current document, by reducing the space available to write the answers:

Interviewer Date Number

Village Division
Altitude :

Name:
Age:
Sex: M/F
Number of inhabitants concerned by the household:

How many fields do you have where bananas or plantains are cultivated?

HOME GARDEN – Surface area of the home garden (if possible):
Distance of home garden to the road or path:
Dessert Banana (yes/no)
Plantain (yes/no)
Cooking banana (yes/no)

Number of plantains:
Number of bananas:
Who is responsible for the home garden?
Year when the bananas/plantains were planted?
Other crops, in order of importance – (number of plants):
1).....(.....) 4).....(.....)
2).....(.....) 5).....(.....)
3).....(.....) 6).....(.....)
Varieties banana/plantain (number of mats):
.....(.....) .....(.....)
.....(.....) .....(.....)
.....(.....) .....(.....)
What **chemical** inputs do you use (herbicides, pesticides...)?
Name Quantity
....
What **organic** inputs do you use (cooking left overs, manure...)?
Type Quantity
....
What is the most important constraint for the banana/plantain production in this home garden?
What do you see as the secondary constraint?

[1] This interview was used in the Northwest Province (Anglophone). An identical French interview was used for farmers in the West Province (Francophone). The interviews were administered by the field technicians of the NAERP in the local language of the farmers

FIELD – Surface area of the field (if possible):
Distance of field to the road or path:
Principle crop:
1).....

Secondary crop, in order of importance – (number of plants):
2).....(.....) 6).....(.....)
3).....(.....) 7).....(.....)
4).....(.....) 8).....(.....)
5).....(.....) 9).....(.....)
Number of banana or plantain plants:.....
Varieties of banana/plantain (number of mats):
.....(.....) .....(.....)
.....(.....) .....(.....)
.....(.....) .....(.....)
What is the most important constraint for the banana/plantain production in this field?
Who is responsible for the principal crop?
Who is responsible for the secondary crops?
Year when the bananas or plantains were planted:
What was planted here before the banana/plantain?
If left fallow, for how many years?
What was the fallowed field occupied by during this period?
What do you see as the secondary constraint?
Do you use inputs? (herbicides, pesticides, organic waste, etc)
Name Quantity
....

When new suckers are planted, where do you obtain the planting material?

A) When the suckers come from your own field: Do you look at the health of the mother plant/mat when you choose your planting material?

What determines a healthy mat?

B) When the suckers come from someone else's field, do you look at the health of the suckers before planting or accepting them?

What determines a healthy sucker?

Do you treat your suckers before planting?
If the answer is yes, how do you treat them?

Have you heard of nematodes? Could you explain what they are and what their function is?
Have you heard of weevils? Could you explain what they are and what their function is?

Do you grow coffee on your farm? (yes/no)
If no, have you grown coffee in the past? (yes/no)
Do you think coffee is a profitable crop? (yes/no)
Have you invested in an alternative crop? (yes/no)
If yes, which crop(s):

How do you rate banana or plantain compared to coffee?

1. Less important
2. More important
3. As important
4. Alternative crop

If the following foods were on a table and you were allowed to choose which you could eat, what would you prefer?
(Indicate favorite food and frequency consumed):

	Frequency consumed per week when available			
Plantain	never	once a week	twice or more a week	every day
Achu banana	never	once a week	twice or more a week	every day
Corn	never	once a week	twice or more a week	every day
Rice	never	once a week	twice or more a week	every day
Potato (irish)	never	once a week	twice or more a week	every day
White yam	never	once a week	twice or more a week	every day
Yellow yam	never	once a week	twice or more a week	every day
Cassava	never	once a week	twice or more a week	every day
Ibu coco (taro)	never	once a week	twice or more a week	every day

Are you part of a farmers' cooperative? (yes/no)

Have you ever followed a training workshop/session on banana or plantain? (yes/no)
If yes, what was the topic of this training?

Would you agree to participate in a long-term project with CARBAP? (yes/no)

Annex 2: List of cultivars cited by farmers

Vernacular and common names[1] of *Musa* cultivars grown by farmers of the West (francophone) and Northwest (anglophone) Provinces of Cameroon

Vernacular and common names of *Musa* cultivars grown in the West Province of Cameroon

Banana pamam
Banane/Bananier
Banane à cuire
Banane allemand
Banane cochon
Banane dessert
Banane douce
Banane du blanc
Banane du village
Banane femelle
Banane Gros Michel
Banane petit doigt
Banane plantain
Banane Poyo
Banane tiko / Banana Tikou / Tiko
Bananier number one
Chapou
Deux mains
Dombo yalie
Dombou baket/Dombo baket
Dombou baquet
Dombou fu
Dombou mekietou
Dombou pagam
Dombou pamam
Faux corne
French court
French geant
French long
French moyen
Gros Michel
Kéde Koua
Kedong sing (bananier plantain)
Kelo
Kelo Ka
Kelo tcheu
Kelo tetung
Kelo tsing
Kelo Koua
Kenam (gros doigts)
Kwo Louh
Labot
Long plantain
Makietou (French court)
Makpere
Makpire
Mbango (long doigt)
Mekere
Mekintou
Mekpere (banane dessert)
Mequitout
Mounja
Mutou (plantain court doigt)
Ngouom (Pagam)
Nom inconnu
Ntou
Number (Tikou)
Number one
Pagam (French long) / Pagham
Panama
Panga (bananier plantain)
Petite naine
Petits doigts
Plantain 12 mains
Plantain à faux tronc rouge
Plantain court doigt
Plantain court doigt (variété naine)
Plantain French rouge
Plantain Gabon
Plantain gros doigts
Plantain Letoh
Plantain long doigt
Plantain nom inconnu
Plantain ordinaire
Plantain rouge
Plantain-banane
Poyo
Syndicat (Gros Michel)
Tokout/Toukout (banane cochon)
Trois mains
Variété de Wum
Variété gros doigt et court
Vrai corne

[1] The cultivar names reflect *Musa* spp. diversity as recognized by farmers in the Cameroon Highlands. No attempt was made to identify synonyms. The cultivar names cited by the farmers are given literally. The names may differ from those listed in literature concerning *Musa* diversity, such as the *Musa*logue (Daniells *et al.*, 2001). Names and synonyms of plantains and causes of confused terminology have been discussed in Swennen (1990).

Vernacular and common names of *Musa* cultivars grown in the Northwest Province of Cameroon

3-4 hands plantain
Abacgeh banana
Achu banana
Bakweri banana
Bamgling
Banana
Banana Number 1
Banguh
Big bunch (Nfung)
Boyo
CDC banana
Chumekefe (long finger/long bunch)
Cooking banana
Dwarf
Dwarf plantain
Ebanga
Ekong
Ekongo
Eyiyi
Fagigom (long bunch)
Fequa (Bakweri banana)
Few fingers
Fire banana
Fon(n)yeah
Fongom
Fuhbuh (Achu banana)
Fuhbuh Fukara
Fukechum (long finger)
Gros Michel
Kitong
Kiyuh mbeka (small bunch)
Kiyuh mboh (one hand)
Kiyuh Si/Kiyusih/Kiyuh Sih (big bunch)
Kunwch
Lakata banana
Livernga
Long bunch plantain
Long finger
Matuh 7 hands
Mbong (3-4 long fingers)
Mbong mbong
Medium bunch
Mekintu/ Mikintu/Nkintu
Nchene
Ndeyuh (short bunch)
Ndoboh/Ndombo
Nfong / Nfung
Nfonycah
Nfuayuh (big bunch)
Ngawalah Kiyeh
Ngokembuku
Ngokigumvike
Ngombe Nchene
Ngomfutuh
Ngominkitu
Ngontimbuike
Ngosoke/Ngosoko/Ngosokeu
Ngowishike
Ngum
Ngum Achu
Ngum Akong/Akongo
Ngum Akup
Ngum Asah
Ngum Aseh
Ngum Banana
Ngum Chuki
Ngum Ekieh
Ngum Eseh/Esheh
Ngum Etum
Ngum Konyo
Ngum Tebanga
Ngum-Banga
Ngum-Ekanyo
Ngum-Eyiyi
Njinikom dwarf
Njombe banana
Nsaiyuh (1-2 fingers)
Ntarang
Number one
Okra
One hand
One hand (13 fingers)
Petite naine
Plantain
Plantain (many hands)
Poyo
Poyo bana
Red skin banana
Several hands plantain
Short banana
Short finger
Shweng
Small bunch (Nchene)
Special plantain
Sweet banana
Three finger plantain
Tiko banana
Timbe (short finger)
Tingom
Trong cader/Strong cader
Tungum
Very short banana (?)
Woman plantain
Yugoh (Ngwansah)/Yugoh (plantain)/ Ngowansoh

Annex 3: Nematode population densities in the Cameroon Highlands

Means ± standard deviations of the nematode population densities in *Musa* roots sampled at increasing altitudes in the Cameroon Highlands (data presented in Figure 2.5)

Altitude (m above sea level)	<800		800-1200		1200-1600		1600-2000		Overall	
	HG	F	HG	F	HG	F	HG	F	HG	F
Meloidogyne spp.	300* ± 141	100 ± 48	3411 ± 10723	2282 ± 4161	1306 ± 1411	1085 ± 973	757 ± 845	664 ± 833	2082 ± 6971	1514 ± 2825
Pratylenchus goodeyi	0 ± 0	0 ± 0	7064 ± 13206	7922 ± 15608	11087 ± 12782	9622 ± 11520	12536 ± 13010	14236 ± 23102	9518 ± 13069	9388 ± 15051
Hoplolaimus spp.	167 ± 47	333 ± 95	539 ± 564	666 ± 743	231 ± 286	212 ± 218	150 ± 246	200 ± 315	345 ± 446	397 ± 555
Radopholus similis	3100 ± 3818	167 ± 47	1785 ± 5535	856 ± 3064	399 ± 1763	229 ± 1504	50 ± 196	0 ± 0	947 ± 3798	457 ± 2228
Helicotylenchus spp.	1633 ± 47	1800 ± 2356	2216 ± 6536	609 ± 1783	92 ± 242	42 ± 101	31 ± 90	17 ± 82	963 ± 4284	289 ± 1195
Total	5200 ± 3770	2400 ± 2546	15015 ± 19254	12335 ± 16456	13115 ± 13247	11189 ± 11948	13524 ± 13414	15117 ± 23484	13856 ±15897	12045 ± 15559
n	2	2	78	81	88	91	24	24	192	198

F = field; HG = home garden; *nematodes per 100g fresh root weight;

Annex 4: List of publications

International peer reviewed articles

Vanreusel, A., Clough, L. M., **Jacobsen, K.**, Ambrose, W., Jivaluk, J., Ryheul, V., Herman, R., Vincx, M. (2000). Meiobenthos of the Central Arctic Ocean with special emphasis on the nematode community structure. Deep-sea research I, 47, 1855-1879.

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Willems, M., Houthoofd, W., Claeys, M., Couvreur, M., Van Driessche, R., Adriaens, D., **Jacobsen, K.**, Borgonie, G. (2005). Unusual intestinal lamellae in the nematode *Rhabditophanes* sp. KR3021 (Nematode: Alloinematidae). Journal of Morphology 264, 223-232.

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W. Houthoofd, **K. Jacobsen**, B. Vancoppenolle, A. Coomans, G. Borgonie (2001) Embryonic development of the free-living, marine nematode *Pellioditis marina*. Proceedings of the 13th International C. elegans Meeting, University of California, Los Angeles, USA. 22-26 June 2001.

Volker Braun, Markus Gumbel, Hans-Peter Meinzer, Ricardo Azavedo, Paul Agapow, Armand Leroi, **Kim Jacobsen**, Wouter Houthoofd, Gaëtan Borgonie (2001) Nematode embryonic cell lineages are computationally efficient. Proceedings of the 13th International C. elegans Meeting, University of California, Los Angeles, USA. 22-26 June 2001.

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Jacobsen, K., Maes, L., De Waele, D., Fogain, R. (2005). Study of the host status of twelve common crops of the Cameroon Highlands for the nematode *Pratylenchus goodeyi*. Proceedings of the 17th Symposium of the Nematological Society of Southern Africa, Limpopo Province, South Africa. 22-26 May 2005.

Annex 5: Guidance to undergraduate students

Dutordoir, N. (2004). Effect van de wortelmassa op de schatting van nematodenaantallen in bananenwortels. Faculteit Bio-ingenieurswetenschappen, Universiteit Gent.

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Maes, L. (2005). Host range of the nematode *Pratylenchus goodeyi* on 12 commonly planted crops of the Cameroon Highlands. Faculteit Bio-ingenieurswetenschappen, Katholieke Universiteit Leuven.