Banana Phenology in Relation to Phytophagous Nematodes

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ABSTRACT

Phytophagous nematodes are well known as serious pests of bananas and plantains worldwide. The opposite perspective (i.e., the influence of bananas on nematodes) has been less studied in nematology. Using this approach, the different relationships between the banana phenology and i) root-system development, ii) nematode population dynamics and iii) the management of nematode damage are briefly discussed. The different phases of banana phenology are related to changes at the level of resolution of the root system. Fluctuations of nematode populations are identified as the result of several factors, but clearly the *renovation of the root system corresponding to pulses of root growth* is the main operating factor in the population build-up of the burrowing nematode *Radopholus similis*. Accurate crop loss assessment in relation to nematode damage, especially on bananas, needs a mechanistic approach based on plant phenology in order to separate the effect on growth from the effect on harvest. Implications of the banana phenology are meaningful for both population dynamics and correlative management strategies of nematode damages. Based on these data a new treatment protocol is discussed which is more compatible with sustainable agriculture. The underlying concept is to apply an 'Individual and Selective Treatment' (IST) on an individual plant basis at the right time according to the prominent density-independent factors (e.g., combination of pulses of root growth and climate).

RESUME

Les graves dégâts qu'occasionnent les nématodes phytophages dans les plantations de bananiers et de plantains sont bien connus dans le monde entier. La perspective inverse (à savoir l'influence des bananiers sur les nématodes) n'a pas fait l'objet d'autant d'études en nématologie. Par cette approche, les différentes relations entre la phénologie du bananier et i) le développement des racines, ii) la dynamique des populations de nématodes et iii) la gestion des ravages des nématodes sont brièvement commentées. Les différentes phases de la phénologie du bananier sont liées aux changements au niveau de la résolution

du système radiculaire. Les fluctuations des populations de nématodes résultent de plusieurs facteurs, mais de toute évidence, c'est la régénération du système radiculaire, correspondant à des poussées de croissance des racines qui constitue le principal facteur d'accroissement des populations du nématode mineur *Radopholus similis*. Pour une évaluation précise des pertes culturales par rapport aux ravages des nématodes, il faut, surtout dans le cas du bananier, une approche mécaniste fondée sur la phénologie de la plante afin de distinguer l'effet sur la croissance de celui sur la récolte. La phénologie du bananier a de sérieuses incidences tant sur la dynamique des populations que sur les stratégies corrélatives de lutte contre les attaques de nématodes. Sur la base de ces données, un nouveau protocole de traitement plus compatible avec l'agriculture durable est examiné. Le concept sous-jacent consiste à appliquer un 'Traitement *individuel et sélectif' sur la base de chaque plant au bon moment* en fonction des principaux facteurs indépendants de la densité (combinaison des poussées de croissance des racines et du climat).

INTRODUCTION

All nematodes, whether free-living or phytophagous, are heterotrophic organisms which are linked to autotrophic organisms for their energy supply. If it is well known that phytophagous nematodes can affect plant growth and productivity, the opposite approach (plant influences on nematodes) has been less studied in nematology. In a recent paper, Yeates (1987) reviewed the different effects of plants on nematodes and re-assessed them in terms of the quantity and quality of plant material available to nematodes. It is within this scope that I will try, for the purpose of this discussion, to give an overview of the influence of the banana-plant phenology on the associated phytophagous nematodes.

First of all, there is a need to set the limits to this discussion : on a worldwide scale, climate ranks first in limiting the geographic distribution (latitude, longitude, altitude, insularity...) of plant-feeding nematodes. The different climatic zones will determine the specific occurrence of banana-feeding nematode communities and their varying species prominence (such as *Radopholus similis* (Cobb) Thorne, *Helicotylenchus multicinctus* (Cobb) Golden, *Pratylenchus coffeae* (Zimmerman) Filipjev, Schuurmans & Stekhoven, and *Pratylenchus goodeyi* Sher & Allen (Gowen & Quénéhervé 1990).

On the scale of a field, the different soil characteristics (texture, organic matter content, pH, soil biota...) and the type of cultivated *Musa* attract a peculiar nematode community based on:

i. the endemic nematode species and

ii. the 'imported' nematode species (e.g., *R. similis*, *P. coffeae*) within the banana-plant material or with other associated crops.

In the following discussion, the boundary of the system under consideration will be at the level of resolution of the banana plant, in a theoretically-defined environment with its specific nematode community. Within this boundary, I will attempt to review briefly the different relationships between the banana-plant phenology and i) root system development, ii) nematode population dynamics and finally iii) the management of nematode damage.

Banana Phenology: Definition and Relationship with the Root System

In general terms, plant phenology, as reviewed by Gepts (1987), is defined as the study of the periodical plant growth and developmental phenomena, as influenced by genotype and environment. Therefore, plant phenology can be characterized in morphological terms through the use of growth and developmental scales. As it is well known, plant phenology is influenced by several factors, including genotype, climate, soil, and the biological environment. Nevertheless, other factors being equal, the genotype is the major source of variability in the phenology of a crop plant (Gepts 1987).

Generally, bananas thrive in a hot and humid tropical environment which involves not only a relative continuous development of the root system but also the continuous reproduction of the associated plant pests and pathogens. Phytophagous nematodes use the roots as a food resource, so it seems evident to focus on the root system: its mode of growing, regeneration and decay in relation to overall banana phenology. From a theoretical point of view, banana plants are composed of two entities: an 'annual' autotrophic aboveground part and a 'perennial' heterotrophic belowground part, the rhizome. Most of the research described below was conducted either on dessert bananas or plantains in a hot and humid tropical environment, so it is obvious that some variations in banana phenology may occur either in a different environment or with different banana cultivars such as on highland bananas. It is conceivable that environmental and/or cultivar-based variations primarily affect the rate of development of the banana plant, rather than the overall banana phenology, but this subject needs further studies.

In an attempt to characterize the stage of growth and development of a banana plant, Lassoudière (1977) gave a helpful description of five different phases in the development of a banana plant, from the sub-group Cavendish, based upon the study of both foliar and root development.

i. a 'youthful vegetative phase' under the influence of the mother plant (slow rhizogenic activity independent of the foliar growth); influence which is decreasing (lanceolated leaves enlarging) when nearing the harvest of the mother plant.

ii. an 'independent vegetative phase' with an intense rhizogenic activity and foliar development.

iii. an 'apparent vegetative phase', rhizogenic activity decreases and stops just before flowering. This phase is concomitant with the following 'iv'.

iv. a 'first reproductive phase' (floral differentiation from 2.5 to 3 months before flowering). This is the phase where the number of hands and fingers is defined.

v. a 'second reproductive phase', corresponding to the increase in size of the fruit, but also concomitant with the 'youthful vegetative phase' of the following sucker.

As for intra-plant variation, the rate of progress from one phase to one another is under the influence of several factors such as number of leaves and leaf area, and the cumulative sum of radiation and temperature (Summerville 1944 , Ganry 1980).

These phases of the banana phenology are related to changes at the level of resolution of the root system. The main sucker of the banana clump (the one which will bear the future bunch) produces new roots continuously until flowering (Beugnon & Champion 1966) even if the rhythm of emergence may vary (Lassoudière 1971, 1978). After flowering there is no more noticeable root emergence on this sucker and the rhizogenic activity continues on the following sword suckers of the clump after they have achieved self-reliance (Lavigne 1987), visible by a shift from lanceolated to enlarged leaves. The maximum peak of root emergence is observed during this period (second flush), between the self-reliance and the flowering stage (Lassoudière 1978, Swennen, Wilson & Decoene 1986). These visual changes result from complex physiological modifications in the relationships between the mother plant and the young sword suckers. These modifications correspond to a crucial period in which the mother plant reduces its regulation, through growth-inhibiting factor, over the growth, the leaf production and the leaf width of the young sword suckers (Skutch 1936).

All these factors act on the growth of the root system in terms of emergence, elongation, branching, physiological senescence and on root system functionalities such as anchorage, capacity of absorption, conduction of solutes and *in extenso* of pesticides. These changes at the level of root system obviously have an effect on the nematode population dynamics.

Relationship between Banana Phenology and Nematode Population Dynamics

When considering a defined nematode species in a defined environment (characterized in terms of geographical location, soil type and host-plant), fluctuations in the nematode population is due to the selective action of effective environmental factors on individuals of the population. Field population studies can only give the final outcome of the influence of all interdependent factors (biotic and abiotic) in the environment. Nevertheless, in order to understand these changes in nematode population levels, it is informative to try to rank these factors by order of importance.

At this point in the discussion, I would like to reintroduce Milne's theory of natural control of insect population (1962), lately brought to light in relation to nematodes by Boag (1989) and specifically adapted here to the regulation of phytophagous nematodes on bananas.

In this theory, environmental factors are divided into three categories :

i. the density-independent factors (A) in which intensity of action is entirely independent of density of x.

ii. the imperfectly density-dependent factors (B) in which intensity of action is determined partly by density of x and partly by other variables which may vary independently of the density of x.

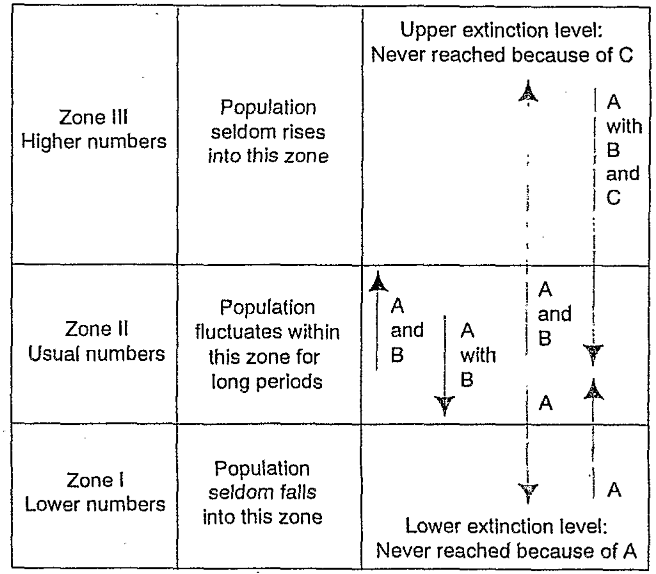
iii. the perfectly density-dependent factor (C) in which intensity of action is determined solely by density of x.

In summary, factor (A) alternates between creating depressive and favorable conditions to nematode fluctuations, while factors B and C are always depressive (Figure 1).

The topic above (of factors that govern dynamics of populations) has been discussed for a long time in ecology and lately synthesized in relation to nematodes by Ferris & Wilson (1987) where additional information can be found. For instance, these authors concluded that density-independent factors are usually, but not exclusively, more predominant and operational than density-dependent factors on nematode population dynamics.

In accordance with these categories, I have surveyed the literature for relevant examples of factors which are proven or highly suspected to act upon the dynamics of a specific nematode species on bananas (Melin & Vilardebo 1973, Jaramillo & Figueroa 1974, Pinochet 1977, Hutton 1978, Mateille, Cadet & Quénéhervé 1984, Sarah 1986; Quénéhervé 1989a, 1989b, 1990). Factors which may be strong influences may be classified as follows:

Figure 1 Theory of natural control of an insect population (From Milne, 1962)



A - Density-independent factors

A1 - Pulses of root growth (food resource) (This factor being directly related to the banana phenology)

A2 - Climate (temperature, rainfall)

A3 - Indiscriminate action of other pests, pathogens and symbionts (interspecific competition excluded)

A4 - Human activities (cultural practices: irrigation, fertilization, application of pesticides, pruning)

B - Imperfectly density-dependent factors

B1 - Other nematode species and/or soil-borne pathogens either competing for the same food resource with direct effect on the abundance and state of food resource (interspecific competition)

B2 - Biological control agents (predators, parasites, pathogens)

B3 - Human activity (pesticide: nematicide treatment)

C - Density-dependent factor

C - Intraspecific competition

In our studies of nematodes on dessert bananas in the Côte d'Ivoire, most of these factors were clearly identified as operating on nematode population dynamics. It is obvious that response levels to factors differ from one nematode species to one another.

For instance, fluctuations of the burrowing nematode *R. similis*, (the primary root invader in the conditions of our studies), resulted from several factors, but the renovation of the root system corresponding to pulses of root growth (a density-independent factor) was identified as the main operating factor in the build-up of the nematode population. Concurrently, many phenomena may occur (imperfectly density-dependent and density-dependent factors) allowing a chronological decline in the population levels and an apparent shift of the multiplication sites from old roots towards new roots (Quénéhervé 1989a,1989b, 1990).

To summarize the relationship between banana phenology and nematode population dynamics, it appears that whatever the nematode species considered, density-independent factors remain the most important and operating factors. It is obvious that similar studies are needed in different environments and with different *Musa* cultivars, such as highland bananas, in an attempt to recognize the environmental factors involved in the natural regulation of phytophagous nematodes.

Relationship between Banana Phenology and Management of Nematode Damage

The production of plant biomass is a complex combination of genotypic, environmental (biotic and abiotic) and genotypic/environmental interactions over time. A mechanistic approach based on crop physiology may permit a better understanding of the interactions which occur between ultimate crop yields and the environment (Gaunt 1987).

Because of the length of development of the the banana plant (from planting to harvest and from harvest to harvest), the different phases of the banana phenology may fall under the influence of different conditions of environment in terms of climate, water and nutrient availability and pest and pathogen pressure. Therefore, crop loss assessment of nematode damage on bananas would strongly benefit from a mechanistic approach based on the banana phenology in order to separate nematode effects on growth as noticed by Gowen in 1975 from their well-known effects on harvest. Using this approach, it has been shown to be possible to refine our understanding of the different components of nematode damages that occur together in dessert bananas (Quénéhervé *et al.* 1991a):

i. Lengthening of the vegetative phases. (Some of the different phenological intervals are lengthened without significant reduction of the bunch weight and number of bunches).

ii. Lengthening of the vegetative phases and reduction of the total harvest. (Two sub-components, reduction of the number of harvestable bunches and reduction of the average bunch weight).

iii. Lengthening of the vegetative phases, reduction of the total harvest and reduction of the longevity of the plantation. (This level is the same as ii) but irreversible due to the loss of plants which are uprooted).

These effects, and especially the first two, are not specific to nematodes and may reflect many other constraints. If the most evident nematode damage is the toppling of plants during the final reproductive phase, the most insidious and neglected damage remains the lengthening of the vegetative phases. On plantain, early and high yields have been reported as results of vigorous vegetative growth (Swennen & De Langhe 1985).

Before considering direct nematode control, nematode damage can be managed in relation to banana phenology through simple cultural practices such as propping fruiting stems with poles to avoid toppling. Another technique is the delayed pruning (until self-reliance) of excessive suckers which can influence nematode fluctuations through recurrent pulses of root growth when the pruning is incomplete (Quénéhervé 1989a).

Nematode control should be conducted in concert with other disease and pest constraints in an integrated pest-management framework and oriented as much as possible towards reduced or non-chemical approaches due to economic and environmental concerns. On bananas, it is obvious that nematode control should only occur:

i. when nematodes are recognized as a limiting factor to the crop, and

ii. within the Milne's theory framework, when the final outcome of the sum-effect of the density-independent factors combined with the imperfectly density-dependent factors is highly favorable to the nematode species identified as the 'key pest' and leads to nematode damages.

Preliminary studies were conducted in Côte d'Ivoire to evaluate the efficacy of new treatment protocols (treatment at harvest to protect the following crop) for chemical control of nematodes on commercial bananas. The concept was to apply an 'Individual and Selective Treatment' (IST) on an individual plant basis:

i. at the right time according to the prominent density-independent factors (i.e., pulses of root growth, climate),

ii. because each banana-plant differs from one another within the field, and

iii. such that only a part of the chemical may selectively be applied rather than the totality of the treatment, depending on soil, rainfall and individual plant conditions.

Both agronomic and nematological results observed during two ratoon crops were very promising; control of *R. similis*, plant growth and yield at harvest were identical to those obtained with the standard treatment of 3 nematicide applications per year (Quénéhervé *et al.* 1991b). This individual and selective treatment (IST), in which banana plants are considered spatially and temporally could be a new approach to banana nematode control, having the following benefits:

i. greater compatibility with low-input agriculture,

ii. greater compatibility with mixed cropping systems,

iii. reduced frequency and cost of nematicide applications,

iv. reduced risk of human and environmental hazards,

v. reduced risk of 'accelerated biodegradation', and

vi. more respectful of the possible biological control agents.

Conclusion

Aspects of banana phenology may be meaningful for both population dynamics and correlative management strategies of nematode damages. Further research is needed on the relationship of root system development, as an aspect of overall banana phenology, to the population dynamics of the different phytophagous nematodes encountered (Quénéhervé 1988, Swennen *et al.* 1988). Besides the quantitative aspects (e.g., root system turnover and production, capacity to form primary, secondary and tertiary roots) leading to an increase of the food resource, the qualitative aspects (e.g., changes in root starch concentrations) and their effects on nematode populations in relation to banana phenology should also be explored. Data, combined from diverse research areas (i.e., soil science, agronomy, plant physiology, plant pathology, plant breeding) are essential:

i. for a better understanding of the ecological relationships and population dynamics of the phytophagous nematodes with respect to banana phenology, and

ii. to improve the management of nematode damages with both cultural and/or chemical strategies compatible with the concept of sustainable agriculture.

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