Eur. J. Soil Biol., 1996, **32** (4), 187-193

Plant-feeding nematodes associated with *Dicorynia guianensis* Amshoff (sub-family Caesalpinioidae) seedlings in a primary rain forest near Paracou, French Guiana

Patrick Quénéhervé [1]*, Moise Bereau [2] and Esther van den Berg [3]

[1] *Laboratoire de Nématologie ORSTOM-INRA, Centre ORSTOM BP 8006, 97259 Fort-de-France Cedex, Martinique (FWI).*
[2] *INRA, Station de Recherches Forestières, Groupe Régional de Guyane, BP 709, 97387 Kourou Cedex, Guyane.*
[3] *National Collection of Nematodes, Biosystematics Division, Plant Protection Research Institute, Private Bag X134, Pretoria, 0001, Republic of South Africa.*
**Corresponding author: Patrick Quénéhervé, Laboratoire de Nématologie ORSTOM-INRA, Centre ORSTOM BP 8006, 97259 Fort-de-France Cedex, Martinique*
Tel 05 96 64 57 50 - fax 05 96 71 73 16
e-mail queneher@nema2.orstom.fr

Received September 23, 1996; accepted March 4, 1997.

Abstract

A recent survey of plant-feeding nematodes associated with seedlings of the forest tree *Dicorynia guianensis* Amshoff in a primary rain forest near Paracou, French Guiana yielded twenty-one species belonging to fourteen genera and one species of an unidentified genus of the Heteroderinae. This plant-feeding nematode population which make up only 7.6% of the total nematode fauna is characterized by i) a high species diversity and equitability and ii) adaptations to feeding on lignous plants, such as having long or robust stylets. The predominant ectoparasites were eight *Xiphinema* and a *Monotrichodorus* species. The predominant endoparasites, extracted from the soil, root mats and seedling roots, were juveniles of an unidentified species belonging to the Heteroderinae, juveniles of *Trophotylenchulus clavicaudatus* (Colbran, 1966) Cohn & Kaplan, 1983 and a semi-endoparasite, *Aorolaimus holdemani* Sher, 1964. All these genera are serious parasites of cultivated plants and trees, especially in the seedling stage. For the first time the possible importance of nematodes in seedling mortality and natural regeneration of a forest tree species was shown in a primary tropical rain forest in South America. Our results of great nematode diversity, are similar to those from other tropical rain forests wordlwide.

Keywords: Cesalpinioidae, *Dicorynia guianensis*, forest tree, French Guiana, plant-feeding nematode, regeneration, South America, tropical rain forest.

Nématodes phytophages associés à de jeunes plantules de Dicorynia guianensis *Amshoff (sous-famille Caesalpinioideae) en forêt primaire à Paracou, Guyane Française.*

Résumé

Au cours d'une récente enquête, 21 nématodes phytophages appartenant à 14 genres différents ont été observés en association avec de jeunes plantules de *Dicorynia guianensis* Amshoff dans une forêt tropicale humide à Paracou en Guyane Francaise. La communauté de nématodes phytophages (seulement 7,6 % de la nématofaune totale) est caractérisée d'un point de vue écologique, par une forte diversité et équitabilité des espèces et d'un point de vue biologique, par une adaptation morphologique à s'alimenter sur des espèces ligneuses (longueur et robustesse du stylet). Les formes ectoparasites prédominantes furent les espèces du genre *Xiphinema* (8 espèces différentes) suivies du genre *Monotrichodorus*, tandis que

Eur. J. Soil Biol.. 1164-5563/96/04/$ 7.00/© Gauthier-Villars

pour les formes endoparasites, extraites à la fois du sol et des racines, prédominèrent une espèce non identifiée appartenant à la famille des Heteroderidae, l'espèce *Trophotylenchulus clavicaudatus* et un nématode du genre *Aorolaimus*. Tous ces genres sont bien connus comme de dangereux parasites des plantes cultivées, mais aussi des arbres dans leurs stades juvéniles. Cette enquête met en évidence pour la première fois le rôle potentiel susceptible d'être joué par des nématodes phytophages sur la mortalité de jeunes plantules et le processus de régénération naturelle d'une essence particulière dans une forêt tropicale humide d'Amérique du Sud. En terme de diversité de la nématofaune phytophage, nos résultats sont similaires à ceux observés dans d'autres forêts tropicales.

Mots-clés : Amérique du Sud, Cesalpinioidae, *Dicorynia guianensis*, essence forestière, forêt tropicale humide, Guyane Française, nématode phytophage, régénération.

INTRODUCTION

The structure and regeneration of French Guiana tropical rain forests were extensively studied by Riera *et al.*, 1990 and Sabatier & Prévost, 1990. Apart from these studies, little is known about the below-ground processes such as rooting habits, symbiosis (Souza Moreira *et al.*, 1992), and associated pest and pathogens. Recently, Bereau & Garbaye (1994) reported for the first time on the root morphology and symbiotic associations of 21 tree species in a tropical rain forest in French Guiana. These authors included information on nematodes in seedling roots of two forest tree species from the sub-family of the Caesalpinioidae, viz. *Peltogyne venosa* Bentham and *Dicorynia guianensis* Amshoff. The present study concentrated on nematodes associated only with *D. guianensis* seedlings, one of the tallest trees in the primary forests of the Guianas area. This tree is of vital importance to the logging industry and in French Guiana it constitutes one third of the total number of trees cut down for timber (Schmitt & Bariteau, 1990).

Plant-feeding nematodes have been recognized as important tree pathogens throughout the temperate zones where they cause losses in forest nurseries and plantations (Ruehle, 1972; Sutherland & Webster, 1993) but little is known of the situation in natural forests, especially in the tropics. Nematode damage is usually visible on forest tree seedlings during the first three years in the nursery. Althought there are many references of nematode-forest tree associations, there have been no reports of widespread damage to adult trees in plantations or natural forests. Information on nematode-forest tree associations in the tropics are scarce. Most references of nematode-forest tree associations comprise description of new species, survey reports (Fortuner & Couturier, 1983; Marais & Buckley, 1993; Price & Siddiqui, 1994) or ecological studies on nematode populations (Hodda *et al.*,1994).

Ecological changes to tropical forests are occurring rapidly, generating considerable interest in the effects of such changes on different aspects (Lieth & Werger, 1989; Whitmore & Sayer, 1992). The objective of this initial investigation was therefore to establish the numbers of, and species diversity of plant-feeding nematodes associated with seedlings of an economically important forest tree species in a natural primary rainforest.

MATERIALS AND METHODS

The study was carried out near the experimental plots of Paracou Forest Reserve in French Guiana, 110 km west of Cayenne near Sinnamary (5°20'N, 52°50'W), an area set aside for forestry research (Bariteau & Geoffroy, 1989). For this survey, six adult *D. guianensis* trees were randomly selected. Underneath each tree, seedlings (ca 1 to 2 years old, up to 30 cm high) were chosen (5 replicates where possible) and carefully removed with a garden trowel together with adhering soil (approximately 400 cm^3 soil/sample) from the root zone, 15 cm deep below the litter layer.

Within four days, the nematodes were extracted from the soil by the elutriation-sieving technique (Seinhorst, 1962) and from the shredded roots in a mist chamber (Seinhorst, 1950) in our laboratory in Martinique. Nematode population levels were determined in a counting dish under a stereomicroscope and expressed either as the number of nematodes per 100 g dry weight of soil or per 1 g dry weight of root (Southey, 1986). Specific identifications of plant-feeding nematodes were performed either on fresh material or on nematodes killed by gradual application of heat, fixed in TAF and permanently mounted on aluminium slides by the slow method of Goodey (1957).

Some simple ecological indices such as the species richness and the diversity and equitability indices of Brillouin (Barbault, 1992) for plant-feeeding nematodes were calculated for each sample. The simplest measure of species diversity is the number of species or the species richness. All the diversity indices are based on the information theory and in the case of definite samples, the appropriate diversity index is given by the Brillouin formula

$H = 1/N \log (N!/n_1!n_2!...n_s!)$ (Pielou, 1972). The equitability E compare the observed diversity to the maximal theoretical diversity $E = H/\log S$. Its value vary between 0 when most of the total abundance is concentrate on one species and near 1 when all species have the same abundance.

RESULTS

Nematodes extracted from seedling soil and roots were grouped according to their feeding behaviour. For the purpose of this study, we distinguished the free-living (88.7±1.2%) and predatory species (4.1±0.7%) from the plant-feeding species (7.6±4.5%). The plant-feeding species belong to the Orders Tylenchida (63.3±5.3), Dorylaimida and Triplonchida.

During this survey, twenty-one species of plant-feeding nematodes belonging to fourteen genera were identified. The species are listed in *table* 1, with, where available, their average stylet lengths recorded from the literature. Among them were three new species, *Helicotylenchus macrostylus, Hemicycliophora paracouensis* and *Xiphinema* n. sp. which are currently being described, while nine species were new records for French Guiana. As illustrated in *table* 1, most of these species have stylet lengths longer than 30 μm, indicating a strong morphological adaptation to feed on thick or lignous root systems, such as roots of forest trees or seedlings. The species with the longest stylets (ca 200 μm) belong to the genus *Xiphinema.*

Up to ten different plant-feeding nematode species were found in and around the roots of one seedling of *D. guianensis* while up to fourteen species were found in and around an adult tree (*table* 2). Juveniles of an unidentified genus of the Heteroderinae were the most abundant among the different sampling sites followed by *Trophotylenchulus clavicaudatus* and species belonging to the genus *Xiphinema*. On the contrary, some species such as *Helicotylenchus macrostylus, Hemicycliophora paracouensis, Mesocriconema* sp. and *Criconemoides ornativulvatus* where found only once at one sampling site. Other species such as *Discocriconemella limitanea, Paratylenchus* sp. and *Rotylenchulus* sp. occurred at two or three sampling sites.

The mean and standard deviation values of the number of plant-feeding nematode in the soil are given in *table* 2. These numbers are fairly similar and

Table 1. – List of the plant-feeding nematodes associated with *Dicorynia guianensis* Amshoff seedlings near Paracou, French Guiana,with their stylet lengths.

	Stylet length (μm)
BELONOLAIMIDAE	
Trophurus vultus Siddiqui & Lenne, 1990	11-14
HOPLOLAIMIDAE	
Aorolaimus holdemani Sher, 1864	29-32
Helicotylenchus macrostylus Marais & Quénéhervé, 1996	42-45
Rotylenchulus sp.	n.a.
HETERODERINAE	
spl-juveniles	n.a.
CRICONEMATIDAE	
Criconemoides ornativulvatus Van Den Berg & Quénéhervé, 1993	74-84
Discocriconemella limitanea (Luc, 1959) De Grisse & Loof, 1965	53-59
Hemicycliophora paracouensis Van Den Berg & Quénéhervé, 1995	103-115
Mesocriconema sp.	n.a.
TYLENCHULIDAE	
Gracilacus sp.	n.a.
Paratylenchus sp;	n.a.
Trophotylenchulus clavicaudatus (Colbran, 1966) Cohn & Kaplan, 1983	11-15
LONGIDORIDAE	
Xiphinema brasiliense Lordello, 1951	197-227
Xiphinema ensiculiferum (Cobb, 1983) Thorne 1937	209-218
Xiphinema filicaudatum Loof & Maas, 1972	308-333
Xiphinema longidoroides Luc, 1961	185-205
Xiphinema cf. *marsupilami* Luc, 1973	270-302
Xiphinema paritaliae Loof & Sharma, 1979	179-207
Xiphinema surinamense Loof & Maas, 1972	201-215
Xiphinema n. sp.	230-261
TRICHODORIDAE	
Monotrichodorus sacchari Baujard & Germani, 1985	56-66

n.a.: Not available.

Table 2. – Abundance (standard deviations in brackets when available) of nematodes associated with *Dicorynia guianensis* Amshoff seedlings in soil (Nb/100 g. dw soil).

Tree	A	B	C	D	E	F
(Nb seedlings/tree)	5	5	1	2	5	5
Free-living species						
Unclassified (fungal-feeder, bacterial feeder, omnivorous)	2781 (1884)	2538 (1532)	2727	689 (675)	1543 (339)	735 (357)
Predators	91 (53)	51 (38)	87	51 (26)	34 (19)	60 (50)
Plant-feeding species						
Aorolaimus holdemani		22		20	3	68
Criconemoides ornativulvatus	35					
Discocriconemella limitanea		51 (31)				
Grasilacus sp.		56 (5)	72	7		7 (3)
Helicotylenchus macrostylus						12
Hemicycliophora paracouensis	49					
Heteroderinae juveniles	47 (47)	44 (24)	22	5 (3)	41 (15)	16 (12)
Mesocriconema sp.		3				
Monotrichodorus sp.	14 (12)	11 (1)				5 (5)
Paratylenchus sp.					7	2
Rotylenchulus sp.		8 (4)		64		
Trophotylenchulus clavicaudatus	17 (14)	20 (10)	109	6		
Trophurus vultus	618	9 (3)				
Xiphinema brasiliense	18 (16)	9 (5)	11		10 (9)	6 (3)
Xiphinema ensiculiferum		7 (2)			3 (1)	3 (1)
Xiphinema filicaudatum	17 (6)	8 (6)	4		12 (9)	2 (1)
Xiphinema paritaliae	38 (23)	17 (10)	7		18 (13)	25 (17)
Xiphinema spp. (other species)	3	4 (1)				3 (1)
Plant-Feeding species (%)	8.8	6.6	7.9	7.3	4.9	8.3

low even for species known for their high numbers in other natural or agricultural environments (e.g. Heteroderidae, *Trophotylenchulus* sp, *Rotylenchulus* sp.). Only one species present in large numbers is *Trophurus vultus*. The percentage of plant-feeding species as opposed to the total number of nematodes present between trees is low, from 4.9% to 8.8%.

Some of the species were found in the root mat where the *D. guianensis* seedlings grow (*table* 3). The Heteroderinae juveniles were only found in the root mat and in the seedling roots together with the *Trophotylenchulus clavicaudatus*. The semi-endoparasite species *Aorolaimus holdemani* was found only in the root mat.

The mean and standard deviation values of species richness, diversity and equitability indices of Brillouin for each tree are summarized in *table* 4. The species richness was more consistent within sets of samples (around a specific adult tree, e.g. species richness highest on tree B) than between sets of samples (among adult trees). The overall diversity of the plant-feeding nematode population can be divided in three group, high around the tree B, medium for the trees A, E & F and low around tree D. The equitability measurements were high and similar for almost all sites, indicating a fairly uniform distribution of plant-feeding species.

Table 3. – Abundance (standard deviations in brackets when available) of plant-feeding nematodes associated with *Dicorynia guianensis* Amshoff in root mat (Nb/1 g. dw roots) and seedling root (Nb/seedling).

Tree Number	A	B	C	D	E	F
(Nb seedlings/tree)	5	5	1	2	5	5
Plant-feeding nematodes extracted from root mat (Nb/1 g dw roots)						
Heteroderinae-juveniles	59 (48)	32 (35)	6	1 (1)	104 (111)	51 (65)
Trophotylenchulus clavicaudatus	41 (36)	39 (45)				
Aorolaimus holdemani				8	2	3
Rotylenchulus sp				17 (1)	6	
Plant-feeding nematodes extracted from seedling root (Nb/seedling)						
Heteroderinae-juveniles	1	8 (2)	27	30	48 (22)	42 (37)
Trophotylenchulus clavicaudatus		4 (2)		27		

Table 4. – Specific richness, diversity and equitability (standard deviations in brackets) in plant-feeding nematodes observed among adult trees of *Dicorynia guianensis* Amshoff.

	Nombre replicates	Richness	Brillouin diversity H'	Brillouin equitability E
Tree A	5	5 (2)	1.52 (0.61)	0.69 (0.24)
Tree B	5	8.6 (1.6)	2.38 (0.41)	0.76 (0.08)
Tree C	1	6	1.76	0.68
Tree D	2	3 (0)	0.91 (0.46)	0.57 (0.28)
Tree E	5	4.2 (1.6)	1.40 (0.34)	0.71 (0.13)
Tree F	5	5.8 (1.3)	1.60 (0.32)	0.63 (0.08)

DISCUSSION

During this study of the nematode community associated with *Dicorynia guianensis* Amshoff seedlings in French Guiana the percentage of plant-feeding species numbers were very low compared to the free-living and predatory species. This result may reflect the relative lower root production and density in the superficial humus layers of rainforest soils compared to the high intensity of decomposition processes leading to a very high number and likely diversity of the free-living species. Our percentages of plant- feeding species are much lower than the 21-33% observed by Sohlenius (1980) in other woodland communities and the 13% (Dorylaimida) and 23% (Tylenchida) found in the Korup Park in Cameroon (Price & Siddiqui, 1994).

Amongst the plant-feeding species, we found the endo- and ectoparasic species to be present in almost equal numbers. The sedentary endoparasites were represented by the Heteroderinae juveniles, the *Trophotylenchulus* and the *Rotylenchulus* species. The swollen females of these genera lay eggs in cysts, egg-masses or capsule-like structures which protude from the root surface. This relative abundance of sedentary parasites seems to be common in tropical and subtropical areas and has also been observed in West Africa with genera of the Heteroderidae (Fortuner & Couturier, 1983; Price & Siddiqui, 1994). In South Africa *Meloidogyne* species are often associated with commercial forests (Marais & Buckley, 1993). In Sao Tome, West Africa, a species of *Trophotylenchulus* is a widespread pest of coffee (Vovlas, 1987).

Aorolaimus holdemani and the new species *Helicotylenchus macrostylus* of the subfamily Hoplolaimidae were also found. Species of this subfamily are obligate plant parasites closely associated with plant roots and can cause root necrosis. They often occur in indigenous forests of West and South Africa (Fortuner & Couturier, 1983; Marais & Buckley, 1993; Price & Siddiqui, 1994) The genus *Aorolaimus* is widespread in tropical and subtropical areas but restricted to South America and some parts of Africa. *A. luci* is also very common in rain forests of the Lesser Antilles (Martinique and Guadeloupe), and has been found associated with ornamental plantations (Quénéhervé *et al.*, 1997) as well as in the coastal area of French Guiana. The species *A. holdemani* and *A. luci* have previously been recorded from Suriname (Maas, 1970). The spiral nematodes (*Helicotylenchus* spp.) are cosmopolitan. They are mostly ectoparasites but may also occur in the cortical tissues. Some of these species are known as severe pathogens of a wide variety of subtropical and tropical fruit trees (Cohn & Duncan, 1990).

Members of the Criconematidae are migratory ectoparasites, feeding on the root cortex of woody perennials in forests and damp habitats. They can also occur in grassland and as severe pathogens on tropical fruit trees (Cohn & Duncan, 1990) and temperate deciduous fruit and nut trees (Nyczepir & Halbrendt, 1993), e.g *Mesocriconema xenoplax* on peach in North America. This adaptation to feeding on woody plants is reflected in their long stylets. In the present study, four species belonging to four genera were observed. One of these genera, *Discocriconemella*, is very common in forest soil of South America and in the Lesser Antilles while *Criconemoides ornativulvatus* was found for the second time since its description from forest soil in Martinique (Van den Berg & Quénéhervé, 1993). Criconematid genera were also the most abundant plant nematodes in indigenous forests from South Africa (Marais & Buckley, 1993).

Members of the Trichodoridae are also migratory ectoparasites of perennial and woody plants. The characteristic "stubby-root" symptom is a result of nematode feeding just behind the root tip, causing a browning of epidermal tissues and a cessation of root elongation, sometimes interfering with mycorrhization. Some species are known to be virus vectors. Monodelphic trichodorids such as the species *Monotrichodorus sacchari*, commonly found in French Guiana, are thought to be native and restricted to Central and South America (Rashid *et al.*, 1985).

The ectoparasitic *Xiphinema* spp. with their long stylets belong to the Longidoridae and they feed on a large variety of host plants. Similar to the Criconematidae, they feed on the root cortex of woody perennials, but also occur in grasslands and

can be severe pathogens on temperate and tropical fruit and nut trees (Cohn & Duncan, 1990; Nyczepir & Halbrendt, 1993). Results of nematode attacks at or near the root tip can cause hooked root-tips and/or terminal galls. Usually, root systems are stunted, lack developed lateral roots and show necrosis at the feeding sites. Sutherland & Webster (1993) regard *Xiphinema* spp. and members of the Trichodoridae as some of the most pathogenic nematodes to forest nursery seedlings, causing root rot. In the present study, this genus was the mots diverse with up to 8 different species at one sampling site. This is also the most diverse *Xiphinema* community reported so far.

As an exemple of the plant diversity in forest stands in French Guiana, studies on the composition of the flora showed that 68 plant families and over 1,050 plant species occur, with at least 10% of the tree species still undescribed (Sabatier & Prévost, 1990). As mentionned by Price & Siddiqui (1994), there should be an incidence of the tree species on the associated nematode diversity (e.g. varying from 7 up to 42 nematode species in their study depending of the tree species). With 156 taxa belonging to 119 genera extracted from the rhizosphere of 23 different tree species these authors described the most diverse nematode community so far.

With regards to the plant-feeding nematode species our results conform closely to similar studies reported in the literature. We found 12 species of Tylenchida and 9 species of Dorylaimida from one site and one tree species. Price and Siddiqui (1994) reported 17 Tylenchida and 4 Dorylaimida species from 23 different tree species at one site in the Korup Park in the Cameroon and Fortuner & Couturier (1983) reported 17 Tylenchida and 7 Dorylaimida species from 26 different tree species at one site in the Taï forest in the Ivory Coast. When more sites are studied the diversity increases, e.g. Marais & Buckley (1993) found 52 Tylenchida and 18 Dorylaimida species from 35 indigenous forest sites in South Africa. More recently D. L. Coyne (pers. comm.) found 27 Tylenchida and 8 Dorylaimida species from 41 forest sites near Gagnoa in the Ivory Coast. Thus, with more intensive surveys on other forest tree species and sites in French Guiana we could expect an even more diverse nematode population.

The plant-feeding nematode community associated with the roots of *D. guianensis* seedlings is morphologically well adapted to feed on lignous plants as evidenced by their long and robust stylets. This nematode population is similar to those already observed in other subtropical and tropical forests. These plant-feeding nematodes can damage seedlings directly, or interact with fungal pathogens and alter mycorrhizal relationships. Diverse, mostly specific symptoms of nematode damage include sparse, stunted, galled, stubby or misshapen roots, leaf chlorosis, retarded growth and stunting and accelerated decay of shoots. Many studies based on Koch's postulate have demonstrated the detrimental effects of plant-parasitic nematodes such as damping-off and root rot of seedlings (Sutherland & Webster, 1993). According to the literature on forest nematodes in temperate climates, ectoparasitic species always outnumber endoparasitic species and genera such as *Paratylenchus, Pratylenchus, Tylenchorhynchus, Trichodorus* and *Xiphinema* are often the most abundant. Species of *Xiphinema* and related genera are the most destructive to forest nursery seedlings (Sutherland & Webster, 1993). As the tree seedlings are obviously more susceptible to nematode damage than adult trees, one can reasonably hypothesize that these micro-agregates of plant-feeding nematodes are able to interfere with the normal growth of the seedlings, often leading to mortality of the plants. As already observed by Bereau and Garbaye (1994), some of the seedlings exhibited features such as brown, swollen and stubby roots, set upon a very poorly developed root systems lacking lateral roots. Seedling roots, after germinating in the litter, have to settle permanently through the dense 5-10 cm-deep root mat covering the soil underneath the litter. During this period (1 to 2 years) the shoot-root ratio of seedlings is highly unfavourable to roots and the root system is confined to the soil layer where plant-feeding nematodes are abundant. These biological processes are concurrent with the natural tree selection which is acceptable and necessary for the global equilibrium of an unexploited natural forest but can become critical when adult trees are exploited for logging such as adult trees of *D. guianensis* in French Guiana. Therefore further detailed studies and observations are needed to validate these assumptions by the demonstration of nematode damage on nursery seedlings.

Acknowledgements

N. H. Buckley , K. P. N. Kleynhans, A. Swart and M. Marais of the P.P.R.I., Republic of South Africa and P. Topart and S. Marie-Luce of ORSTOM, Martinique, are thanked for technical assistance and the identification of different species.

REFERENCES

Barbault R. (1992). – Ecologie des peuplements. Structure, dynamique et évolution. Masson, Paris, 273 p.

Bariteau M. & Geoffroy, J. (1989). Sylviculture et régénération naturelle en forêt Guyanaise. *Revue Forestière Française*, **16**, 309-323.

Bereau M. & Garbaye J. (1994). – First observations on the root morphology and symbioses of 21 major tree species in the primary tropical rain forest of French Guiana. *Annales de Sciences Forestières*, **51**, 407-416.

Cohn E. & Duncan L. W. (1990). – Nematode parasites of subtropical and tropical fruit trees. *In*: Luc, M., Sikora, R. A. and Bridge, J. (Eds), *Plant-parasitic nematodes in subtropical and tropical agriculture*, CAB International, Wallingford, 347-362.

Fortuner R. & Couturier G. (1983). – Les nématodes parasites de plantes de la forêt de Ta (Côte d'Ivoire). *Revue de Nématologie*, **6**, 3-10.

Goodey J. B. (1957). – Laboratory methods for work with plant and soil nematodes. *Tech. Bull. Minist. Agr. Lond.*, **2** (3rd ed).

Hodda M., Bloemers G. F., Wanless F. R. & Lambshead P. J. D. (1995). – Nematodes and carbon fluxes in tropical forest in Cameroon: preliminary results. *In*: Nilsson L. O., Huttl R. F., Johansson U. T. Mathy P. (Eds), *Nutrient uptake and cycling in forest ecosystems*, Ecosystem Research Report 21. Commission of European Communities, Brussels, 131-137.

Lieth H. & Werger M. J. A. (1989). – *Tropical rain forest ecosystems: biogeographical and ecological studies*. Oxon, UK, Elsevier.

Maas P. W. Th. (1970). – Tentative list of plant parasitic nematodes in Suriname, with descriptions of two new species of Hemicycliophorinae. *Bulletins Van Het Landbouwpoefstation*, N° 87, 9 p.

Marais M. & Buckley N. H. (1993). – Plant-parasitic nematodes in forest soils in the Transvaal and Natal, *South Africa. South African Forestry Journal*, **166**, 9-16.

Nyczepir A. P. & Halbrendt J. M. (1993). – Nematode pests of deciduous fruit and nut trees. *In*: Evans K, Trudgill D. L. & Webster J. M. (Eds), *Plant-parasitic nematodes in temperate agriculture*, CAB International, Wallingford, 381-425.

Pielou E. C. (1972). – Niche width and niche overlap: a method of measuring them. *Ecology*, **53**, 687-692.

Price N. S. & Siddiqui M. R. (1994). – Rainforest nematodes with particular reference to the Korup National Park, Cameroon. *Afro-Asian Journal of Nematology*, **4**, 117-128.

Quénéhervé P., Van den Berg E., Topart P. & Hostachy B. (1997). – Analyse écologique de la spécificité parasitaire des nématodes phytoparasites associés à quelques plantes ornementales cultivées à la Martinique. *Nematologica*, **43**, in press.

Rashid F., De Waele D. & Coomans A. (1985). – Trichodoridae (Nematoda) from Brazil. *Nematologica*, **31**, 289-320.

Riera B., Puig H. & Lescure J.-P. (1990). – La dynamique de la forêt naturelle. *Bois et Forêts Tropicaux*, **219**, 69-78.

Ruehle J. L. (1972). – Nematodes of forest trees. *In*: Webster J. M. (ed) Economic Nematology. Academic Press, London-New York, 312-334.

Sabatier D. & Prévost M. F. (1990). – Quelques données sur la composition floristique et la diversité des peuplements forestiers de Guyane Francaise. *Bois et Forêt Tropicaux*, **219**, 31-55.

Schmitt L. & Bariteau M. (1990). – Gestion de l'écosystème forestier Guyanais. Etude de la croissance et de la régénération naturelle. Dispositif de Paracou. *Bois et Forêts Tropicaux*, **220**, 3-23.

Seinhorst J. W. (1950). – De betekenis van de toestand van de grond voor het optreden vanaantasting door het stengelaatje (*Ditylenchus dipsaci*) (Kuehn) Filipjev. Tijdschr.Plziekt, **5**, 291-349.

Seinhorst J. W. (1962). – Modifications of the elutriation method for extracting nematodes from soil. *Nematologica*, **8**, 117-128.

Sohlenius B. (1980). – Abundance, biomass, and contribution to energy flow by soil nematodes in terrestrial ecosystems. *Oikos*, **34**, 186-194.

Southey J. F. (Ed.) (1986). – *Laboratory Methods for Work with Plant and Soil Nematodes*. Reference Book Ministry of Agriculture, Fisheries and Food No. 402, London, Her Majesty's Stationery Office: 202 p.

Souza Moreira F. M., Da Silva M. F. & Faria S. M. (1992). – Occurrence of nodulation in legume species in the Amazon. *New Phytologist*, **121**, 563-570.

Sutherland J. R. & Webster J. M. (1993). – Nematode pests of forest trees. *In*: Evans K, Trudgill D. L. and Webster J. M. (Eds), *Plant-parasitic nematodes in temperate agriculture*, CAB International, Wallingford, 351-380.

Van den Berg E. & Quénéhervé, P. (1993). – *Criconemoides ornativulvatus* sp. n. from Martinique (Nemata: Criconematinae). *Fundamental and Applied Nematology*, **16**, 539-542.

Vovlas N. (1987). – Parasitism of *Trophotylenchulus obscurus* on coffee roots. *Revue de Nématologie*, **10**, 337-342.

Whitmore T. C. & Sayer J. A. (Eds.) (1992). – *Tropical deforestation and species extinction*. Chapman & Hall, London, UK, 153 p.

EUROPEAN JOURNAL OF SOIL BIOLOGY

formerly - revue d'écologie et de biologie du sol

VOLUME 32 / N° 4 - 1996

1996, 4, 165-203

gauthier-villars