THE JOURNAL OF AGRICULTURE
OF THE UNIVERSITY OF PUERTO RICO

Issued quarterly by the Agricultural Experiment Station of the University of Puerto Rico, for the publication of articles by members of its personnel, or others, dealing with any of the more technical aspects of scientific agriculture in Puerto Rico or the Caribbean Area.

Vol. XLVIII April 1964 No. 2

The Plant-Nematode Problem of the American Tropics

G. Steiner and Edna M. Buhrer[1]

FOREWORD

Before his death, in 1961, Dr. G. Steiner, late Nematologist of this Station, had begun an article which was to have been very comprehensive, perhaps even serving as a textbook on nematode problems of the American Tropics. The junior author has compiled his notes and edited his incompleted manuscript, using the experience gained through her many years of close association with him during his 34 years of service with the U.S. Department of Agriculture. Unfortunately, an outline of the projected paper could not be found among his notes. It is quite possible, therefore, that the material here is not always presented in the order intended. As can be seen in reading, only the initial paragraphs of several of the chapters had been written. In spite of these obstacles publication was thought desirable in the hope that Dr. Steiner's observations, written in the years of his mature judgment and vast knowledge and experience, will add to his many other contributions in the field of plant nematology.

INTRODUCTION

It may appear premature and inopportune to select for a topic a problem which *ab initio* must be based on a restricted volume of work, facts, and knowledge. The science of plant nematodes, however, has entered an era of intensified research and surging interest, has shown a trend toward the American Tropics, and rightly so, and thus deserves specialized attention, however premature it may appear. This is a trend that deserves full support, for it concerns an area of highly promising fundamental agricultural research, with possible broad economic application. The Tropics in general are regions of deficient food production, a fact often discussed and variously explained. The apparent rapid exhaustion of tropical soils under cultivation is usually stressed as a main factor responsible for the situation. Exhaustion

1 Late Nematologist, Agricultural Experiment Station of the University of Puerto Rico, Río Piedras, P.R.; and former Nematologist, Crops Research Division, USDA Beltsville, Md., respectively.

in this instance is interpreted as a depletion in mineral and organic elements. Certain facts and observations, however, are in opposition to such an all-inclusive explanation.

The apparent general restoration of fertility to abandoned cultivated lands of the Tropics, without any application of mineral or organic fertilizers after the virgin vegetation has been reestablished, appears to disprove this exhaustion argument. In addition, still other observations show fallacies in the argument: 1, A change in type of crop may correct the features of exhaustion; 2, certain plants, particularly weeds, may grow luxuriantly on such supposedly impoverished soil; 3, symptoms of exhaustion are prevalent with certain crop types only; or 4, such symptoms are singularly pronounced in monocultures, especially when these are of a multiseasonal or perennial character.

Furthermore, if the land reverts to native vegetation, or to certain types of pasture, signs of exhaustion may disappear. Moreover, virgin and secondary tropical vegetation does not usually show such symptoms of soil impoverishment. Thus the socalled exhaustion argument is at least not a fully satisfactory explanation for the seeming loss of fertility. Why? It overlooks or at least underestimates one most important item, namely, that the world of organisms that these soils harbor is not only a factor of fertility, when as dead corpses they decompose to fertilizing compounds, but that many of these biota are of dominant significance in the intricate relationship between soil, crops, and vegetation. Or, that they are direct noxae, which live on crops and plants, and thus may cause crop declines simulating an exhausted, sick, and impoverished soil.

Plant nematodes belong in this category of soil organisms. The present intensified investigations are an attempt to explore more thoroughly their nature and their significance in the agronomy and the plant life of our American Tropics. Therefore, a review of past work and published results on this subject, and an examination of the present status of the inherent problems as they pertain to the Tropics are not only desirable but a timely necessity. It calls for an assay of what is known, a reexamination of previously and currently accepted concepts, a review of problems that at present appear most significant, and the outlining of programs.

In speaking of plant nematodes I do not restrict the term, as some do, to parasitic and pathogenic forms, but include all nematodes having a direct or indirect relationship to plants, such as nematodes that feed on other plant pathogens or otherwise destroy or influence them, as do the mycetophagous and predatory nematodes; also included are forms that distribute such plant pathogens as bacteria and fungus spores, and forms that are vectors of viruses. Conversely, other organisms that affect plant nematodes in one way or another are also considered. In short, we include under this heading the whole complex of nematode forms involved and associated with plant life and crop production.

Our problem is, therefore, not simply the question of what forms of parasitic or pathogenic nematodes occur on crops in the American Tropics, how they cause damage, and how they may best be controlled, but it is also the problem of the ramified interrelationship between this highly diversified and exceedingly numerous group of organisms and the plant life of our region.

The geographical area covered by our topic is roughly that between the Tropics of Capricorn and Cancer of the Western Hemisphere, with inclusion of the Hawaiian Islands. This territorial expanse is much of a *tabula rasa* in regard to cognizance of the nematodes that populate its soils and vegetation. The few locations in this area where actual research on plant nematodes has been, or is being pursued, are the Hawaiian Islands, some areas in Brazil and Peru, certain islands of the Caribbean, and isolated places in Bolivia, Colombia, Ecuador, Venezuela, Panama, Guatemala, Costa Rica, El Salvador, Honduras, and Mexico.

Results of past work in this territory have been reported in publications that form an extensive list, as shown in the Bibliography which we have attempted to make as complete as possible. This Bibliography is published herewith as an article in this issue of the JOURNAL, and appears immediately following the present article. However, numerically impressive as this Bibliography appears, it covers the subject and territory most fragmentarily. A few single nematode noxae of plants, particularly root knot nematodes, and only a restricted number of crops are covered, such as pineapple, banana, coffee, sugarcane, coconut palm, cotton, kenaf, potato, and certain vegetables. Comprehensive investigations on entire nematode associations on crop plants, fields, and native vegetation are nonexistent.

This, of course, reflects a concept of the overall problem that has been dominating agronomy, soil science, plant pathology, zoology, and even the thinking of certain specialists in the very field of plant nematology. Nor is it limited to the American Tropics. It is the notion that there are just a few significant nematode pests of plants and that only certain specific crops are subject to their depredations. This view ignores the absolutely ubiquitous occurrence of plant nematodes, their large and diversified numbers, their continuous inroads upon crops and vegetation, their complex role in soil life, and, indirectly, their influence on the behavior of a soil. It thus has become a prime requisite that this antiquated concept of the problem of plant nematodes be up-dated, especially as it concerns our American Tropics.

We hope that plant pathologists, soil scientists, agronomists, foresters, horticulturists, economists, sociologists, administrators, and governments may eventually realize the significance of the living component in tropical soils as a factor that is primarily responsible for the pattern of native agriculture, variously called bush-culture, slash-and-burn cultivation, or shifting cultivation. To ignore this basic fact will further condemn to failure any attempt to improve food production and subsistence agriculture in our Tropics.

THE OVERALL PROBLEM

The presence of nematodes in all agricultural lands and wherever plants grow and vegetation occurs is an established fact. It is certainly true for our Tropics. From personal experience I can substantiate that, in these Tropics, croplands abound with nematodes. Both the past and current interpretation, however, of this teeming world of organisms rank them as mainly saprobionts. As stated above, nematode types living on plants, or affecting them in one way or another, are thought to be few, of sporadic occurrence, and to be restricted to certain crops, while the bulk of the forms associated with roots and other underground parts of vegetation are thought of as having no connection with plant life. One needs only to peruse treatises on the subject of agriculture in general, and of our region in particular, to find that, with few exceptions, nematodes have been either completely ignored, or dealt with as a matter of curiosity and of little import.

It is my aim to point out the fallacy of such notions and to attempt to establish a broader and more realistic understanding of this factor, "nematodes", as it operates in our tropical crop husbandry and regional vegetation. A sojourn of some months at the Instituto Agronomico in Campinas, Sao Paulo, Brazil, and at present, studies in Puerto Rico extending over some years, have provided opportunities for an "on-the-spot" acquaintance with the problem. I have collected evidence that, in these Tropics, plant- and crop-attacking nematodes of many kinds are present everywhere, that agricultural lands often harbor fantastic numbers, and that in these aggregations the forms that live on plants are predominant.

There usually exists a concentration in numbers and types in the root expanse of plants, specifically in the top strata of the soil; their taxonomic makeup is normally and preponderantly that of a stylet-bearing, plant-feeding species—not dominantly a saprobic type. Comprehensive analyses of the composition of such nematode associations in our region are still lacking. Their group significance and the compatibility of the associated forms are not yet understood, nor is that of the entire association of life forms. We have been too much engrossed in taking out of these associations certain single types for study, and have meanwhile forgotten the rest of the forms and the association itself. Yet, to understand the life in the biotopes concerned, we must consider the whole as well as all its parts, particularly as we attempt to understand how damage to our crops is effected, and how it may be alleviated.

To my knowledge it was N. A. Cobb (fig. 1) who first was intrigued by

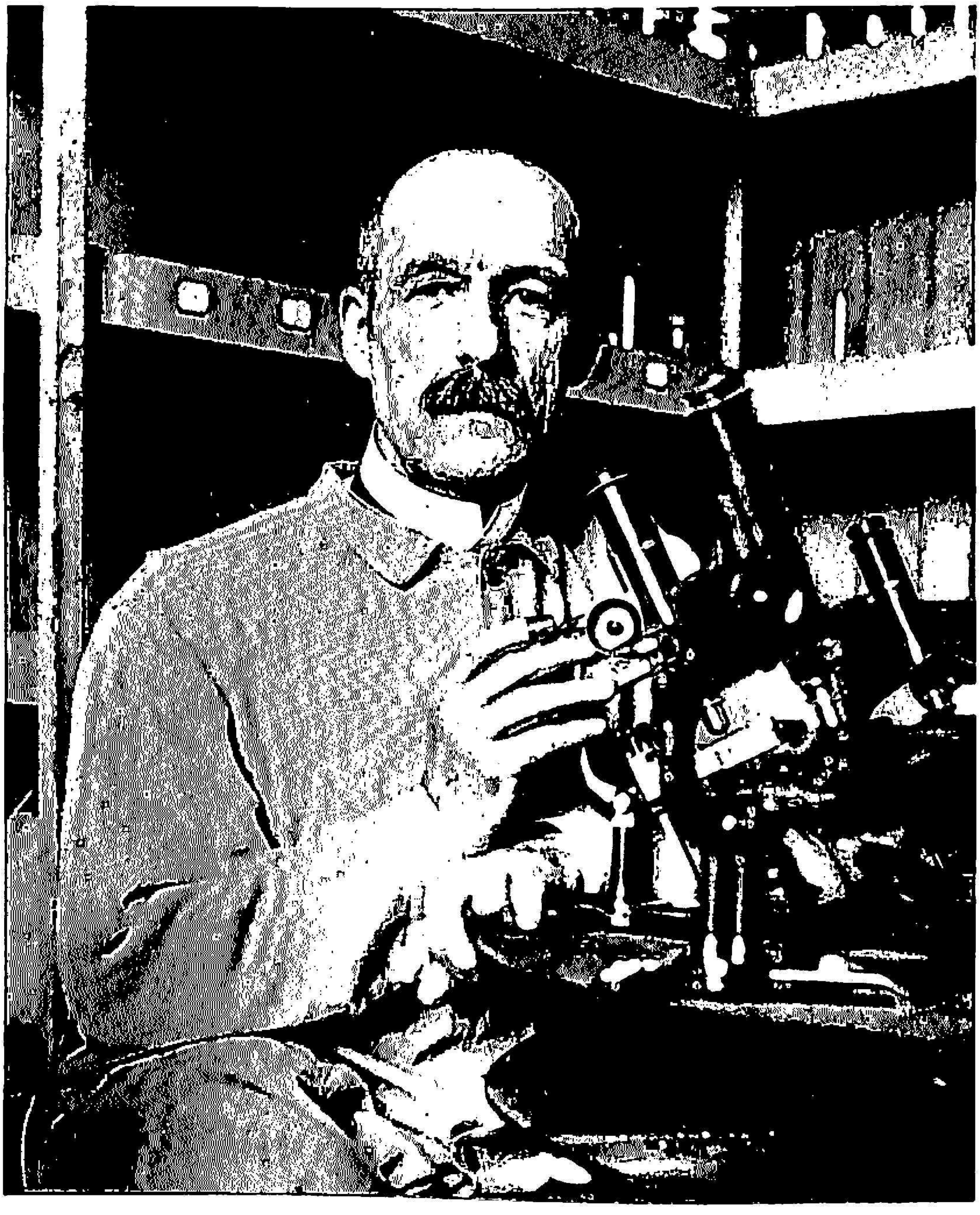

FIG. 1.—Nathan Augustus Cobb, 1859–1932.

the concentration of nematodes in the root expanse of certain crop plants, and who tried to interpret its significance in relation to crop and plant behavior. At that time he was working in Hawaii, especially on sugarcane, and therefore with a plant of the region under discussion. At the start of the present century Cobb took charge of the Pathology and Physiology Division of the Experiment Station of the Hawaiian Sugar Planters' Association in Honolulu, then newly established. He was no novice with nematodes. Since his student days with Häckel in Jena he had been greatly impressed by the ever-present and teeming world of these helminths in all kinds of environments, including the agricultural soils. Although his official work, first in Australia, and then in Hawaii, centered on other problems, he always had surplus interest and enthusiasm to devote time to these fascinating organisms.

Working in Hawaii with fungal root diseases of sugarcane Cobb also took cognizance of the associated nematodes—a quite unusual procedure for those days—and his reflections thereon were quite ahead of his time. We quote (Cobb 1906, p. 163):

> A prominent feature in the life of every stool of cane is the growth and decay of its roots. At a comparatively early age the roots begin to die off, and are constantly replaced by new ones. We have come to regard this as a normal and entirely unpreventable phenomenon.
>
> Nevertheless, there seems to be no natural reason why, of itself, a root should decay. The most probable supposition is that these roots are attacked by some parasite and die in consequence. If this is so, any measure that forestalls the parasite will stave off the demise of the root.
>
> In the soil-inhabiting nematodes we seem to have organisms perfectly capable, through their punctures, of giving entrance to smaller parasitic organisms that would hasten the death of plant roots.
>
> I have examined the soil about the roots of cane on many occasions, and in several different countries, and have described nearly fifty species of nematodes found in this situation. The great majority of these species are such as feed upon the roots of the cane, securing their food by puncturing the epidermis and sucking out the juices of the root through the puncture thus made. The wounds made in this way must commonly reach a very high number. It is not unusual to find hundreds of these little creatures about a single stool of cane. The habits of many of them are such that the daily number of their punctures must be large. It seems to me that each wound made in this way is quite likely to encourage the entrance of parasitic plants, either microbes or fungi, whose presence in the roots would mean death.
>
> All this is, of course, somewhat in the nature of a speculation, but if the grounds on which it is made are well taken it justifies further inquiry as to the habits of soil-inhabiting nematodes. It is quite possible, in my opinion, that what we call fairly healthy and well-to-do plants may yet sustain such a draft on their resources in combating the attacks of soil-inhabiting nematodes that were they relieved of this strain their resulting growth might surprise us.

So wrote Cobb in 1906, but outside of Hawaii little attention was given to the nematode complex associated with sugarcane roots, for the nematode type almost exclusively considered was only root knot.

Sugarcane appears to be a plant of strong attraction to numerous kinds of root-attacking nematodes. In Puerto Rico one regularly observes a whole array of such forms in and on the stools of cane, representing dozens of taxonomically different root-feeders, such as spiral nematodes (*Helicotylenchus* spp.), meadow nematodes (*Pratylenchus* spp.), root knot nematodes (*Meloidogyne* spp.), stylet nematodes (*Tylenchorhynchus* spp.), pin nematodes (*Paratylenchus* spp.), ring nematodes (*Criconematinae*), stem nematodes (*Ditylenchus* spp.), sheath nematodes (*Hemicycliophora* spp.), bud-and-leaf nematodes (*Aphelenchoides* spp.), dagger nematodes (*Xiphinema* spp., *Longidorus* spp.), stubby-root nematodes (*Trichodorus* spp.) and *Trophurus* spp. Thus the aspect of sugarcane root stools in Puerto Rico presents a picture similar to the one described by Cobb from Hawaii. Stools often exhibit root rot to such a degree that one wonders how the plant is able to survive and to grow (fig. 2). Particularly in older plantings, fantastic numbers of these nematodes may be seen, often amounting to many millions per square meter. As shown by an analysis of the genera and species present, stylet-bearing and known root-attacking forms markedly prevail. Their relationship to the observed necrotic condition of these sugarcane roots appears evident, but actual experimental proof is wanting.

Our current work, however, has shown that sugarcane roots are not only very attractive to numerous nematode types, but are also of delicate sensitivity, and are easily damaged; necrosis is a regular result of nematode invasions and attacks. To what degree this necrosis is induced by nematodes only, or whether it is a result of a combination of nematodes and fungi or bacteria, or still other agents, has not yet been ascertained. In Puerto Rico it is apparent that root knot is of wide occurrence and extremely detrimental to sugarcane plantings, but is not usually noticeable through gall formation on the roots. If galls are formed at all they are few and small, mostly terminal. Nevertheless, it appears that root knot nematodes are a significant factor in root decay.

T. van der Vecht (1949, p. 64) mentions a similar situation from the region of Bogor (Buitenzorg), Java, where at first root knot seemed not to occur on sugarcane, but eventually was found to be quite generally distributed, after it had been established that the knots or galls, thought to be a typical feature of this disease, were not formed. The root rot induced had quite generally been ascribed to fungal, bacterial, and viral factors only. Cobb's and later Gertrude Henderson Cassidy's attempts to call attention to the significance of the nematode factor in sugarcane production have hardly been noticed. (See also J. H. Jensen *et al.*, 1959). Root rot of cane as here referred to must also occur in other cane regions of our Tropics and wherever sugarcane is grown (see *e.g.* Vallance, 1959, p. 21).

Almost a duplication, for example, of our figure 2 may be seen in a paper by D. B. Pickel (1938, p. 363, fig. 1) dealing with a root disease of cane in Pernambuco, Brazil. Unfortunately, in this instance no effort had been made to search for a nematode factor as the cause of this *mal da raiz*. That the roots of the seed-piece of sugarcane should be short-lived, die, and rot with the seed-piece after the latter is exhausted, appears natural, but that the roots of the rhizome and of individual shoots should be ephemeral, and be constantly replaced as a normal course of matters is certainly questiona-

FIG. 2.—Nematized root of sugarcane taken from nontreated field soil in Puerto Rico. Photograph from collection of the senior author.

ble. Experiments in progress show that, under nematode-free conditions, cane stools form root systems free of the above-mentioned decay; such root systems have long, white feeder roots, much in contrast to the blackened, stubby and moplike formations so frequently observed where dead roots prevail (fig. 3).

FIG. 3.—Healthy sugarcane root systems showing long, white feeder roots. Photo courtesy of W. Birchfield, U. S. Department of Agriculture.

These facts and considerations lead to the question of how, then, sugarcane is still raised economically, and in reality still forms the backbone of many tropical agricultures and economies? Undoubtedly, this has been made possible through a kind of cane husbandry that has developed unknowingly, together with applied methods which are very effective in controlling cane-antagonistic nematodes and similar biota. It is the procedure of replanting cane fields as often as production drops to an uneconomical level. Replanting in this instance consists of plowing, disking, redisking, and applying other methods of thorough physical and chemical preparation of a field. If these measures are analyzed for their effect on the nematodes and other biota of the old cane stools and their soil, it becomes evident that they are very destructive measures, and therefore reduce nematodes and other biota quite efficiently.

Mechanical destruction of the old stools and their roots, their drying and decay, deprives all root-feeders of their food and eliminates them by starvation. Furthermore, it kills and reduces many forms through such means as shrinkage of the roots and their tissues before the endoparasites have been able to move out, through the production of inhibitory or even toxic gases and soil solutions, and through lack of oxygen. Mechanical disturbance of the soil, therefore, has its impairing and often lethal effect on the nematodes. Insolation has long been known to be very detrimental to them. Fertilizers, insecticides, herbicides, and manures all exert a more or less impairing, frequently killing, action. The destructive effect of a hurricane on the aboveground vegetation and life community is generally recognized; but the far more destructive action of plowing, disking, redisking, subsoiling, compaction, and other types of cultivation on soil life strangely has never been openly appreciated nor fully considered.

It is evident that, in the ways just indicated, the procedure of replanting effects a reduction of soil biota and particularly of plant nematodes. The only studies in our region concerning part of these problems are those of Linford, Yap, and Oliveira of 1938. H. Franz and others, however, have reported on studies concerning certain soil-management procedures in Central Europe (Austria). Manures and mineral fertilizers were shown to have had a very profound modifying and partly eliminating effect on nematode populations in fields of that country. There is no reason to assume that the same effect is not also produced in the Tropics and, as stated above, observations in cane fields support such a conclusion.

The above-described decline of cane under uninterrupted production is not unique to this crop; it is a phenomenon of general occurrence. The inherent problems, however, are singularly well exemplified in sugarcane husbandry, in its many nematode attackers, and in its cultural features and requirements.

Up to the present the significance of replanting as a practice in sugarcane husbandry has almost entirely been considered a method to improve the physical and chemical character of the soil, so that the cane plant may again grow better; to a lesser degree the rejuvenescence of the plants has also been visualized as a side-effect. But the control action on the soil life and its noxae has not been specifically appreciated nor emphasized. Yet we see in it one of the reasons, perhaps the main one, why cane is one tropical crop grown in continuous monoculture that seems to form an exception to the concept: tropical soils under cultivation need a rest period achieved by a return to virgin or secondary vegetation so that their fertility may be restored.

Another crop of our Tropics that is grown under somewhat similar conditions of husbandry is the pineapple. In this instance the significance of the factor nematodes has been more realistically recognized and evaluated, although not to its fullest extent. Efforts to overcome the noxious effect of nematodes have been directed at their elimination, and have culminated in the wide use of nematocidal soil treatment as a basic procedure. Pineapples are also grown in continuous culture, *i.e.* without a rest period that is thought to reestablish the assumed exhaustion of soil fertility. In this regard it is suggestive to quote Collins (1960, p. 265):

> Pineapple and sugarcane have been grown for many years in Hawaii without crop rotation or green-manure crops, and appear to be exceptions to the general need for crop rotation in order to maintain yields. Nevertheless, when pineapples and sugarcane were alternated on the same soil in Kauai, a mutual increase in yields resulted.
>
> One plantation in Hawaii for many years grew a green-manure crop of a tropical Panicum grass for 18 to 24 months between pineapple cycles. Pineapple yields have increased since this rotation has been used. The dense growth of grass prevents weed growth and thereby reduces weed-control costs in the following crop of pineapples. In addition, this grass is not a host for the root-knot nematode, and consequently these pests are greatly reduced during the intercycle period.
>
> Both Australia and South Africa use green-manure crops alternating with pineapples. It is probably significant that these green-manure crops produce better results on the following pineapple crop when they occupy the soil for about as long as the preceding pineapple crop.

In this way Collins emphasized that, in Hawaii, it has been possible to produce sugarcane and pineapples for many years without rotation or green-manure crops. No specific reasons are given to explain why this has been possible, and why yields have been maintained in contrast to the otherwise-accepted need of rotation and green-manure crops. That, in the culture of pineapples as well as sugarcane, the procedures incident to replanting might be a factor to this end, is not recognized. In both crops the procedure is very similar and has doubtless a similar effect on various nematodes and other soil biota. Collins mentions the benefit of a panicumgrass rotation only in crowding out weeds, and in reducing the incidence of root-knot nematodes, but the overall effect of replanting and rotation is not viewed as wholly or partly connected with general control of nematodes and other soil pests.

It is surprising that this continuous production in monoculture of sugarcane and pineapple has not been considered in discussions on the causes of loss of fertility of tropical soils through cultivation. Neither has it been contrasted with the method of growing subsistence crops by slash-and-burn cultivation, bush-culture, or shifting cultivation—different terms for fundamentally selfsame procedures. I refer here to the method of producing these crops by clearing and burning the virgin vegetation from patches of land, then planting to subsistence crops, usually a mixture and in succession, for 1, 2, or 3 years, and eventually abandoning the land again, so that secondary vegetation may return to reestablish the fertility that it is assumed was exhausted by the preceding period of cropping.

Shifting cultivation in its various modes has often been discussed (see, *e.g.*, the presentation by P. Gourou, 1954, or the more recent one by P. H. Nye and D. J. Greenland, 1960, or FAO Staff, 1957). Since it is a practice applied by the natives all over the Tropics there are many native terms for it and its modifications. In the American Tropics, the "Milpa" system is in use in Guatemala and Yucatan, the "Coamile" in Mexico, the "Canuco" in Venezuela, the "Roca" in Brazil, etc. It is not my intention to discuss these various modes here, but I would like to point out that one phase of the effect of shifting cultivation has been overlooked almost completely in all debates on the merits and demerits of the system, namely, its significance as a means of reducing and avoiding the effect of soil pests, particularly of noxious nematodes.

The socalled quick exhaustion of tropical soils has all the features of soil fatigue (*Bodenmüdigkeit*) and crop fatigue caused by nematodes. The very term "soil fatigue" ascribes loss of fertility erroneously to the soil proper, and implies some structural or chemical defect rather than the presence of noxious organisms as the cause of yield declines. Nematodes often produce this phenomenon, although this has not been recognized in the Tropics, notwithstanding its basic significance for an understanding of shifting cultivation. Nye and Greenland (1960, p. 75) considered this phase of the problem very sparingly. They listed the reasons a farmer might be induced to abandon a piece of land and clear another for better cropping as follows:

1, Multiplication of pests and diseases.
2, Increase of weeds.
3, Deterioration in the physical conditions of the soil.
4, Erosion of topsoil.
5, Deterioration in the nutrient status of the soil.
6, Changes in the numbers and composition of the soil fauna and flora.

Thus the authors give a full coverage of all the different groups of crop-antagonistic factors, but in their discussions they do not equitably analyze and evaluate the various items. The paragraph on Pests and Diseases is the shortest and may be quoted here to demonstrate how the soil biota are inadequately viewed as factors of crop declines:

The long rest given to the land during the fallow, the scattered distribution of the small plots, and the fact that one kind of crop is rarely grown more than once in each cropping period—all these factors serve to check the build-up of pests and diseases, and it is seldom that the period of cropping is curtailed because of them. Pests and disease might well multiply if the cropping period was extended so that one crop was grown at frequent intervals. For example, in the forest region of Ghana, it is possible to follow the maize planted in the early rains with a second crop in the late rains. When this is done the second maize crop will frequently be seriously affected by corn-stalk borer (Bowden, 1956).[2] Traditionally the farmer has not planted a second crop of maize, possibly for this reason. Again, in the savanna region, the opening crop is frequently yams. A second yam crop is rarely grown; when it is, it is often seriously affected by yam beetle (*Heteroligus meles* and *H. claudius*). Experiments described by Cutting *et al.* (1959)[3] in Nyasaland, where 'head smut, stalk borer and striga in maize, and root eelworm of tobacco are rampant in areas of prolonged African cultivation', have shown clearly the advantage of rotations. Maize, groundnuts and tobacco all yielded better in rotation than in monoculture. Indeed, the advantages of rotational systems in controlling pests and diseases seem in general to be reflected in customary native cropping sequences.

Thus nematodes are recorded only in connection with tobacco, and the forms obviously referred to are root knot nematodes. The existence of a large complex of other types of nematodes is not even mentioned. Under the heading Changes in the Soil Fauna mainly arthropods are referred to and, in this instance, cultivation is thought to reduce the population that was originally present when the land carried its virgin vegetation. There is, however, an extensive discussion of items 1, 4, and 5, which demonstrates that, in searching for reasons why shifting cultivation has been developed, and why it became the one method practiced over the entire Tropics from time immemorial, soil biota are assigned only a fragmentary and restricted role, whereas structural and chemical, particularly nutritional, properties of the soil are considered principal factors. A defective explanation this is, yet it is the gist of so many discussions on the failure of tropical agriculture to provide sufficient food for the people of its lands. In this regard it is interesting to refer to the appeal made by the Food and Agriculture Organization (FAO) of the United Nations to "governments, research centers, associations and private persons who are in a position to help" (see FAO Staff 1957).

To us this situation is the result of a misconcept of tropical soils in regard to their life component. As elementary and significant a part of these soils as are the nematodes, they have been misjudged, even overlooked, as anti-

[2] Bowden, J., Maiz stem borer control extension dusting trials, first and second seasons, 1954, *Ghana Farmer*, 1 23–26, 59–61, 1956.

[3] Cutting, C. V., Wood, R. A., Brown, P., and Ambrose, H. B., Assessment of Fertility Status and the Maintenance of Productivity of Soils in Nyasaland, Paper No. 69, Third Inter-African Soils Conference, Dalaba, 1959.

fertility factors. The omniprevalence of nematodes in tropical soils, their taxonomic diversity, plus their equally multifarious relationship to plant life, are of the highest significance and are basic to the production of subsistence crops. It is only with a consideration of these facts that a full understanding of shifting cultivation is possible. Therefore, an analysis of the effect of this type of cultivation on the nematode component and the ensuing crop is essential. We must face the fact that a patch of land that has been under virgin vegetation or secondary growth for a period of 10 or more years produces a satisfactory yield of subsistance crops, whereas an old patch having been in use for 1 to 5 years will not do so.

Virgin vegetations as well as aged secondary ones are largely of mixed composition. It has been stated that some 50 or more different species of trees may be found growing on an acre of virgin forest. This means that the nematode fauna on such an area must also be, and in fact is, highly diverse, since so many different types of hosts are present. The old concept of largely omniphagous plant-nematode species is erroneous; I hope to have an opportunity to demonstrate this on such plant pests as the root knot nematodes, the meadow nematodes, the burrowing nematodes, and many others. This has a bearing in the present case. The nematode fauna of a mixed vegetation is composed of many more different types than that of a monoculture and, as far as my observations go, also of many more other life forms such as tardigrades, mites, and collembola.

It has also been stated that in virgin and secondary forests seed of trees do not grow under their own shade. This is a situation easily understandable if viewed from the nematode angle. Such seed will be attacked at their germination by the same nematodes that live on the roots of the parent tree, because of the identity of hosts. An invasion of the young rootlets will mutilate or destroy them and so prevent a seedling from undergoing proper development and establishment. If such a patch of land is taken under cultivation the method followed will be that of cutting and burning the vegetation. This will deprive the nematodes of their food and force them to transfer to one of the subsistence crops, or if unable to do so, to perish. Only a minority of the originally occurring forms will survive and develop. The burning over of the patch of land will further kill or impede many nematodes near the soil surface by heat, by compaction, or by the vastly modified soil solution which will be saturated with solubles from the ashes or dead organic materials.

Under most methods of shifting cultivation the mere mechanical disturbance wrought upon a soil will be minor; reduction of noxious nematodes by this mode of control must therefore be minor also. However, shifting cultivation has other features that are antinematocidal. Subsistence crops, for example, are regularly grown in mixed cultures, often not even in rows or patches. This practice impedes the spread and propagation of their specific nematode attackers. It thus is evident that shifting cultivation has one outstanding feature that hitherto has been largely ignored; its significance as a means of controlling soil nematodes.

ECOLOGICAL BASIS OF PLANT-NEMATODE PROBLEMS

Plant nematodes do not usually occur in assemblies of a single taxon. Rather, the root expanse of plants regularly harbors multifarious associations of nematode types. To single out one or more noxious forms, perhaps on the basis of their numbers or their pathogenicity, and apportion to them the crop behavior and the damage observed would be only partly appropriate; it would neglect the effect of the entire association of nematodes for analysis of the decline or disease condition.

Such analysis, however, must embrace not only the nematodes, but also other associated biota such as the fungi, bacteria, viruses, insects, mites, tardigrades, annelids, turbellarians, rotifers, gastrotrichs, and protozoans, to say nothing of the chemical and physical environmental factors and the traits of the host and associated plants. Such entities must be weighed as: The soil structure, soil-mineral and colloidal constituents, quantity and nature of soil organic matter, soil air, moisture, and temperature, together with the fact of their continual change and of their annual cycle. Still other points to be assessed are exposure to insolation, shade, or wind, to the type of soil management applied, and the soil amendments made, etc.

Most important are the plants themselves, their traits and denouements. Roots and other underground parts, such as rhizomes, tubers, corms, and bulbs, are of many morphological and physiological types. They thus affect nematodes in many different ways and to varied degrees. Their consumption of water, minerals, and gases differs, and so does their production of carbon dioxide. In addition, their production of effluviums and diffusates varies much in kind and amount, as does that of enzymes and auxines. All these entities pertaining to the rhizosphere of plants influence its biota and certainly also its nematode components.

The rhizosphere is a dynamic system and the phase that comprises the immediate contact zone of soil and root is particularly significant as a locus of nematode concentration and activity, and hence of plant-nematode interrelations. In this contact zone there usually prevails a concentration of microbial life forms, such as bacteriorhiza and mycorhiza, producing thereby high metabolic activity. Here the root has its nutritive stratum which often surrounds it as a more or less continuous casing. Here also is that association of diverse nematode types—not only such as feed on the roots. The space outside this direct contact zone also has its biota, including nematodes, but it is a dispersed field of interaction though equally related to the root system.

Here mention must also be made of the phenomena of antagonism between organisms, for they are of particular importance in soil life. Antagonism between organisms may reveal itself in many ways and to many degrees, from retardation to inhibition of growth, to toxic and to even lytic effects. Factual knowledge in this domain, as far as our plant nematodes are concerned, is restricted. Some investigators have tried to interpret certain crop disorders as the result of crop antagonism, whereas others see in them a nematosis.

Some, for example, claim that slow decline and also spreading decline in citrus plantings, and *Müdigkeit* or "soil fatigue" in fruit-tree nurseries, and similar phenomena, are cases of "isoantagonism." This refers to the antagonism between organisms of one kind as contrasted with "heteroantagonism"—the antagonism between organisms of different taxonomic status. Isoantagonism is best exemplified by the phenomenon of a bacterial or fungal organism that stops growing because of the "staling" of the medium, and is interpreted as the result of self-toxication, or self-inhibition by its own metabolites. In the case of the citrus decline and nursery soil fatigue it is assumed that citrus trees and fruit trees also produce metabolites that are inhibitory or toxic to themselves. This assumes a citrostatic effect to parallel that of a bacteriostatic and fungistatic effect in cultures of these organisms. Present evidence does not support such a contention. Citrus declines and soil fatigues have convincingly been demonstrated to be related to nematode attacks.

Heteroantagonism as a phenomenon in plant-nematode ecology has been explored specifically only in relation to predators, and then only in relation to food competitors and forms producing antibiotics. It is strange that only antibiotic effects between plants should be considered as a possible explanation in observed noncompatibility, when actually interference by nematodes and other soil biota may also be examined as factors. Reference is made to a recent discussion of such a problem by J. R. Cannon *et al.* (See Bibliography that follows).

Other traits of roots, significant in relation to plant nematodes, are growth tempo, age, lignification, lifespan, etc. Plants with fast-growing and extensive root systems are more likely to escape a relevant damaging effect by any attacking nematodes. Frank, as early as 1884 (pp. 155–6) remarked that plants with strong ability to regenerate roots are less likely to be harmed than slow root-formers. Most susceptible are the young, still-growing roots. Seedlings that are invaded before they have established a good root system may die; plants invaded after being established often suffer little. Transplants set in heavily infested soils may never be properly established because their young rootlets are immediately attacked, blinded, and inactivated.

Plant-nematode infestations also have an historical aspect, data on which may contribute essentially to the cognizance and understanding of the current status. Particularly helpful are crop and vegetation histories, information on past rotations, soil managements, and soil amendments. All these items may have to be examined in an attempt to evaluate fully the nematode factor in a disease decline or deportment analysis of crops, plants, and vegetations. The complexity of such an undertaking is evident.

It is thus a mistake to assume that a specific nematode, be it a parasite, a pathogen, or just an associate in an ecological complex, should always have the same effect, when actually the associated agents and environmental factors regularly are of a varying nature and combination. We fully recognize the need and duly appreciate the attempts to solve soil biotic problems by plate cultures. We must never overlook the fact, however, that isolation of single and multiple factors in all kinds of ingenious setups are largely artifacts compared with the actual field situations.

It thus becomes trite to emphasize that problems concerning soil biota and soil life are almost hopelessly complex, especially their nematode fractions. The disregard of these basic facts has been the cause of many misinterpretations and misjudgments of field aspects in relation to plant nematodes. Not infrequently, for example, the same deleterious nematode type has been judged a serious factor of decline and again, as of no significance. Such seeming contradictions have often been the result of a failure to recognize first, the taxonomic diversity of nematodes and second, the entirety of other conditioning agents and factors involved in a case. Plant-nematode problems are to be studied and acted upon on the basis of the entire ecological situations and not only on that of isolated single noxious nematode types.

PARASITISM OF NEMATODES ON AND IN PLANTS

There is a consensus of opinion that an entirely satisfactory general definition of parasitism is difficult, in fact, has not yet been formulated. This status applies to the parasitic relations of nematodes to plants. It is difficult to establish here a dividing-line between a noncompulsory and a compulsory association of nematodes and plants, and to determine where parasitism begins and free association ends. One of the reasons for this situation is our ignorance concerning the food and the feeding habits of many of the nematodes we observe associated with plants, especially with plant roots. Nematodes are fundamentally sucking organisms. Their mode of feeding is an ingestion by suction through contraction of radially arranged muscles of the pharyngeal tube, evolved from one by ciliar action.

A muscular pharynx doubtless is more efficient than one provided with cilia only, because larger quantities and sizes of food morsels may be swallowed.

Parasitism of nematodes on plants may not be expressed in a single equation that is applicable in all instances. This parasitism is very gradual in its effect, and also is otherwise very diverse. The effects may extend all the way from an unnoticeable impairment of the host plant to the opposite extreme of pronounced injury. Its diversity in types is rich, and climaxes in some most remarkable interrelations of host and parasite. It must be emphasized that the disease-producing effect of parasitic nematodes on attacked plants is not accounted for by nutrient depletion alone, nor by that of mechanical injury or mechanical interference; it includes as a major phase the physiological disturbances wrought upon the plant by nematodes through their active injection of digestive and related compounds into the host. It includes also the passive excretions, secretions, and gaseous exchanges resulting from metabolic processes.

Investigators must also be aware of the fact that plant nematodes may be internal as well as external parasites. They may enter the tissues of an attacked plant completely and either settle down at a convenient inside location permanently (= sedentary endoparasites) or move through the tissues (= migratory endoparasites). In contrast, some may feed on a plant from the surface by puncturing the tissues or only partly entering (= ectoparasites); among these some may settle down permanently (= sedentary ectoparasites), while others may move around and feed sporadically (= migratory ectoparasites). But again, modifications of many kinds occur in each of these groups. It is interesting to note here that, in contrast to their parasitism on plants, nematodes have never developed any significant degree of ectoparasitism in animals.

To understand this contrast one must keep in mind that ectoparasitism on plants is made possible by the presence of moisture in the tissues around the nematode in the attacked plant parts. Nematodes are fundamentally aquatic animals; moisture in the form of surface films, capillary moisture, or tissue moisture, is the customary biotope. Disappearance of moisture induces dormancy and even prolonged anabiosis. Soil water, as commonly spoken of, is actually a solution of salts and other ingredients and hence of greatly diversified makeup. How the nematodes are affected by, and react to, these variables is a neglected subject, but it would be remiss to assume a nonresponsiveness to these diverse media. It is unfortunate that there also exists an almost complete lack of information as to how manures, fertilizers, weedkillers, soil amendments, insecticides, and other pesticides influence plant nematodes and other soil biota.

SEDENTARY PARASITES

As mentioned above, plant nematodes have developed some remarkable modes of parasitism, phenomena that deserve attention as curiosities among biological systems. Let us consider first the tissue parasitism of root knot nematodes (*Meliodogyne* spp.). It has few comparable counterparts that demonstrate equally well the astute structural and functional interplay of two organisms tied together as host and parasite. It shows how a parasite may exploit to a most astounding degree the faculties of a host, and adapt itself to unusual conditions. The following may demonstrate some of the fascinating phases of this parasitism, and simultaneously outline the inherent problems.

A juvenile root knot nematode is guided to its host by specific chemical messengers contained in root or other tissue secretions dispersed in the soil solution. These chemical messengers are perceived by an extremely fine and highly effective perceptory apparatus, the amphidial organs. These organs are a combination of a glandular cell plus a nerve that leads to a sensillar terminal apparatus located in a pouch- or flasklike structure having a circular or a slitlike opening at the surface of the head. This structure bears some resemblance to the taste bud of the human tongue and is assumed to have a somewhat similar function, namely that of analyzing the soil solution for scents of host plants and also of the sexual partner.

Moving toward the source of a secretion by following its increasing strength, the juvenile root knot nematode will arrive at the root tip of a host plant. The extraordinary functional capacity of this chemical sensory apparatus for detecting the scent of its host is well shown by the nematode's ability, in instances, to distinguish between varieties of a host plant. Since root knot nematodes are endoparasites the root is entered by the juvenile, but not at any casual location. Penetration occurs in a section just proximal of the calyptra in the region of growing meristematic tissue.

The juvenile nematode then migrates, ostensibly using intercellular space to avoid tissue damage, to the vascular bundle where it settles down to a sedentary life. Its anterior end is directed proximad, its tail end toward the root tip, its dorsal side toward the root axis, its ventral side with the excretory pore and anus (and in the adult female, the vulva) toward the root surface. A remarkable feature of this placement within the root is that the head end is turned dorsad, *i.e.* toward the vascular bundle, and that the stylet point, which at first is straight, also becomes dorsally curved during the third and fourth molts (see fig. 4). This stylet point is replaced at each molt, a fact that makes possible its change in form; in contrast, the stylet shaft is not molted, and thus retains its straight shape. When the juvenile nematode is thus established it is ready to initiate feeding.

A study of the structural interrelations of parasite and host at this stage, and of the changes that now occur, shows that the juvenile parasite obviously stimulates growth and tissue modifications of its host, particularly in the region adjacent to the oral opening. These stimulations are produced by the injection of secretions of the dorsal pharyngeal gland of the nematode, the outlet of which is located immediately behind its buccal stylet. Of the three pharyngeal glands present in root knot nematodes the dorsal one is the largest; the two subventral ones are not only smaller, but differ

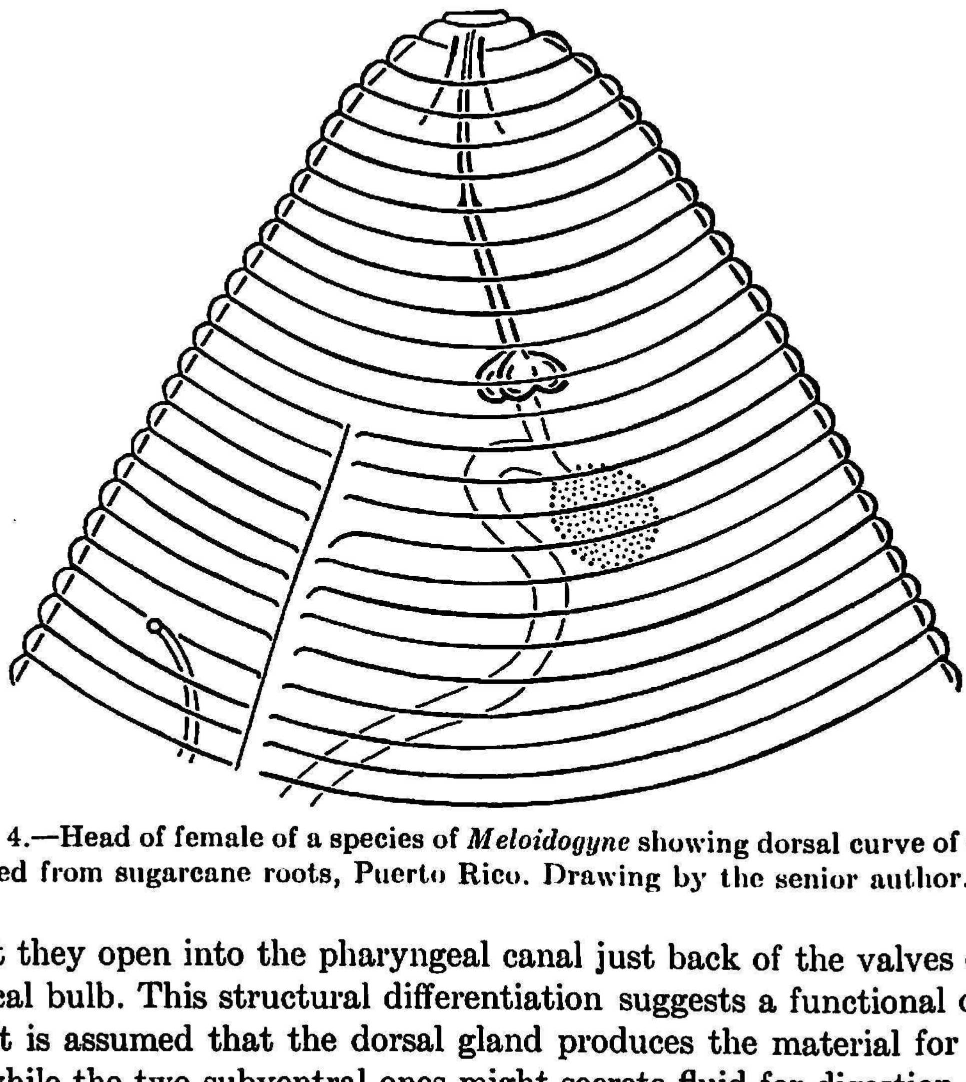

FIG. 4.—Head of female of a species of *Meloidogyne* showing dorsal curve of stylet. Collected from sugarcane roots, Puerto Rico. Drawing by the senior author.

in that they open into the pharyngeal canal just back of the valves of the spherical bulb. This structural differentiation suggests a functional one as well. It is assumed that the dorsal gland produces the material for injection, while the two subventral ones might secrete fluid for digestion of the ingested food. True or not, there is the fact that the nematode induces the plant to form the socalled giant or nectarial cells which are located closest to the oral opening, and which usually number 3 to 5. From these giant-cells the nematode obviously gets its food in fluid form.

It is known that the pharyngeal glands function throughout the life of the nematode. Their action therefore is not restricted to the transformation of the host tissue into gall tissue, but is continuously effective in inducing the incessant production of food by the plant host. We have termed the combined functions of the pharyngeal glands as peri- or extraoral digestion. Whether this is a complete digestion or only a partial one, and in what way the two types of glands take part in the process, and how the giant or nectarial cells function, are unsolved questions.

Other cells in the region of the giant-cells of the host plant are also affected by the secretions of the nematode. These secretions have various effects on plants, some responding with the formation of large-sized, others of smaller galls, some with no gall formation at all, others with necrosis. But this is only part of the complexity of the present phenomenon.

Another phase is the problem of how the plant host and its tissues take care of the metabolic products of this endoparasite, such as its gaseous and digestive wastes, its molts, its eggs, and its young. The position of the nematode in a root, with the ventral side toward the root surface, is interpreted as adaptive, since it appears to make for better elimination of not only metabolic wastes, excretory and anal, but also brings the eggs and juveniles closer to the root surface and the outside of the root.

A still more striking feature of the present type of parasitism is the sexual dimorphism of these root knot nematodes. Although some of these forms may propagate at least over some generations without males, in other instances males are of common occurrence. The genetic mechanisms at work here have not been analyzed. The males *per se*, however, are quite remarkable in their participation in the present type of parasitism. As stated above, the juvenile root knot nematode begins its sedentary parasitic life inside the tissue of the host. Its growth is predominantly by increase in width so that eventually a more or less spheroid body form is reached, with the anterior end forming a kind of protuberance.

In the female the transformation of the body from a filiform shape in the juvenile to a more or less spherical form in the adult, and coincidentally, a shift of the vulva caudad to near the anus and tail end, induces the cuticular structures, as well, to adaptive modification. Thus the annulation, which, in the juvenile, is regular throughout the body length, is partly squeezed out, or is folded through these changes; as a result the characteristic but diverse patterns of marking around the vulvar and anal openings are produced. It was Carl Müller (1884) who first noticed and discussed this shift of vulva and anus to the tail end, and also published a drawing of the pattern.

Nematodes as far as known are cell-constant organisms, *i.e.*, growth after development is only by enlargement of the somatic cells, not by their multiplication. This, of course, does not apply to the generative cells. As the adult stage of these sedentary nematodes is reached the globulose body of the female is unable to move, and the possibility of mating appears remote.

It is here that a most interesting differentiation between female and male maturation occurs. The female does not change its apple- or pear-shaped form, and remains at its location.

The male, however, an equally swollen growing juvenile, initiates a maturity growth in length, so that within the last molt (cast cuticle) a vermiform, cylindrical, folded male nematode develops. This male is eventually able to move out of its cast and migrate through or out of the tissues of the root in search of the female. Not only has the form of the body been changed and a nematoid shape reestablished, but other structures also have reverted.

The annulation has reverted to the regular type; the lateral fields are fully and normally developed, not more or less obliterated as in the female; the head has become broad, rounded, large, and much stronger than that of the female; the amphids are much enlarged and obviously more developed both structurally and functionally; the buccal stylet is much stronger, its point less distinctly curved; the procorpus of the pharynx is cylindrical, not swollen as in the female; the metacorpus bulb is smaller, usually oblong rather than spherical; the pharynx and intestine are distinct; the nerve ring is distinct and has a normal form; the three pharyngeal glands are long and overlap the intestine ventrally in tandem. The intestine appears to be a compact body without a distinct cavity and with few large cells. The cloaca, anus and male gonopore, is subterminal. It is also of special interest that the postcloacal (postanal) region of the body in *Meloidogyne* males is not annulated, thus to some degree paralleling the smooth vulvar-anal-caudal plate of the female.

The sexual dimorphism of *Meloidogyne* poses the question of its significance, indicated by the return of the male to motility, and by its structural and functional adaptations that enable it to locate the female and to copulate. Although an actual copulation has not yet been observed in *Meloidogyne*, there appears to be no doubt that it occurs. This is concluded from the finding of males near females and in or around egg-masses. It appears improbable that nature would have produced all these adaptive structures and functions for no purpose, particularly such extraordinary features as the twist or torsion of the body of the *Meloidogyne* male, understandable only as an adaptation to make possible a more effective copulation. Since the female has a globose body with the vulva at the posterior curvature, the twist of the filiform body of the male doubtless helps to increase the hold of the female by the male. Most interestingly, there are species of *Meloidogyne* with males that have no torsion, others with the beginning of a 90° torsion at the tail end, and then torsions of 180° up to 900°, or 2½ full torsions, the steps of increasing torsion always being of at least 90°.

Records of the occurrence of root knot nematodes in our Tropics are mostly from cultivated areas. However, root knot does occur in virgin lands, although records of such distributions are few, possibly because such searches are rarely made. We have seen root knot on *Hevea* seedlings collected in the jungle of the Amazonas region and on a wild sweetpotato in a virgin forest in Riberao Preto, Sao Paulo, Brazil. There exist many different species of root knot nematodes in the American Tropics. It is historically noteworthy that this group of nematode parasites was first described from the Tropics of our Western Hemisphere.

An entirely different type of parasitism is seen in forms of the genus *Rotylenchulus* Linford and Oliveira, 1940, the reniform nematodes. The female is a sedentary ectoparasite while the male is free-living and has no parasitic stage. The juveniles of both sexes reach maturity in preparasitic life and copulation presumably takes place at this stage. It plainly is a case of paedogenesis. The fertilized female then proceeds to establish itself on a root, the head end being inserted into the root tissue and reaching the vascular cylinder, where food is sucked in and probably also digested extra-orally. The female then attains a size many times that of the sexually mature juvenile; the ovaries and gonoducts then develop fully. In this case paedogenesis replaces the developmental dimorphism as seen in the *Meloidogyne* male.

The reniform nematodes are among the most numerous and widely distributed kinds of nematodes in Puerto Rico, and appear to be prevalent forms in Hawaii also. Information on their occurrence elsewhere in our region is lacking. Attainment of sexual maturity and mating and death of the male before parasitism are unique phenomena in the world of plant nematodes, and present a sequence of problems, such as the mode of molting and the process of growth after sexual maturity in the female in relation to an assumed cell constancy as in other nematodes. The citrus nematode, *Tylenchulus semipenetrans* Cobb, 1918, demonstrates a quite similar type of parasitism.

MIGRATORY PARASITES (*Radopholus* SPP., BURROWING NEMATODES)

This group of nematodes now classed under the generic name *Radopholus* Thorne 1949, has been most extensively studied in the American Tropics and the adjoining region of the US. *R. similis* (Cobb, 1893), which must be considered the type species, was originally found on bananas in Fiji. The genus represents a most interesting group of migratory, endoparasitic, root- and rhizome-attacking nematodes.

In the American Tropics burrowing nematodes are most widely known as root pests of bananas (*Musa sapientum*), plantains (*M. paradisiaca*), and sugarcane (*Saccharum officinarum*). Lists of other hosts have been published from the Hawaiian Islands and Florida. *Radopholus* is common on bananas and plantains in Puerto Rico, and has been observed on coffee and a number of ornamentals. It is remarkable that up to the present no *Radopholus* has been seen on citrus in Puerto Rico, nor elsewhere in citrus-growing areas other than Florida.

Sugarcane has been reported attacked by these pests only from the Hawaiian Islands and Louisiana. We have not yet seen them on this host in Puerto Rico.

These nematodes have not been reported on bananas outside the American Tropics, including Florida, and the Fiji Islands.

There seems to be a host-range distribution that demonstrates behavior differences concerning hosts, and suggests the possibility of the presence of a group of species, rather than of a single taxon as it is presently conceived. Furthermore, there is a discrepancy in the available descriptions of *Radopholus similis;* even the descriptive statements of Cobb differ when his three reports are compared in detail. Presently two or three species are classed in this genus: *Radopholus similis* (Cobb, 1893) Thorne, 1949, *R. oryzae* (Breda de Haan, 1902) Thorne, 1949, and *R. gracilis* (deMan, 1880) Hirschmann, 1955.

The genus was diagnosed by its author, Thorne, as follows:

> Pratylenchinae. Two ovaries present. Head of female resembling that of *Pratylenchus pratensis*, with low lip region set off by a slight narrowing of the head contour, about half as wide as base of neck. Female spear also very much like that of *P. pratensis*, about twice as long as lip region width with strong basal knobs. Esophageal gland lobe extending back over intestine. Phasmids of both sexes prominent, located well back of the tails. Deirids not observed. Bursa enveloping only about four-fifths of tail. Tails of both sexes elongate-conoid to the rounded or irregular shaped terminus.

A diagnosis that is better formulated might be: *Radopholus* = Tylenchinae, amphidelphic, pharyngeal glands overlapping anterior intestine dorsally or subdorsally, bursa not enclosing tail end, pronounced sexual dimorphism.

The history of these taxa is briefly this: N. A. Cobb, in 1893, established the species *Tylenchus similus* on the basis of the male only, for which he furnished five figures, the locality (Fiji), and the host (banana). It is a species with the following male characters: 1, Head with 7 annules; 2, lateral fields ¼ body-width, with 4 bands, 2 narrow edging ones and 2 wider inner ones (see Cobb, 1893, pl. 42, fig. 4 of *Tylenchus similis*); 3, buccal stylet distinct, conical, not like stylet of males as shown in Cobb, 1915, p. 567; 4, tail 4× length of spiculum; 5, gubernaculum convex, thinner in middle, slightly swollen at both ends; 6, male tail end, in fixed specimen, dorsally curved (see Cobb, 1893, figs. 3, 4, and 5). In 1906 he described and figured more fully *Tylenchus biformis* from sugarcane roots in Hawaii;

males and females were at hand and showed a pronounced sexual dimorphism; but the great resemblance of the male to that of *T. similis* was not noticed, at least no mention was made of such.

Tylenchus similis of Cobb 1915 differs from *T. similis* Cobb, 1893 by the male's having: 1, 8–10 striae (= 9–11 annules) on the head instead of only 7 annules; 2, through its buccal stylet, which is very weak, difficult to see, and lineate, not conical and plain as in *T. similis* Cobb, 1893; 3, lateral fields having only 3 bands, being wider (⅓ or more of body width, as against ¼ in *T. similis* of Cobb, 1893).[4]

MILIARY, ORGAN-TISSUE, AND INTRACELLULAR NEMATODES IN PLANTS

Little thought has been given to the significance of nematodes as the cause of disease in the plant as a whole. Not only the cause, but also the mechanism and the effect of these various types of nematodes are quite unknown. The case of *Ditylenchus dipsaci* (Kühn) Filipjev in the teasel (*Dipsacus fullonum*) is, as such, the only known example. No instance of a miliary nematosis in a tropical plant is known. The closest to the condition in our Tropics is the red-ring nematosis of the coconut palm.

The red-ring disease is caused by a remarkable nematode that was originally described as *Aphelenchus cocophilus* Cobb, but later reclassified as *Aphelenchoides cocophilus* (Cobb) Goodey, and still later as *Rhabdinaphelenchus cocophilus* (Cobb, 1919) J. B. Goodey, 1960. It is a form of unique character. Structurally the slenderest endoparasitic plant nematode known, it is reported to live in the roots, the stem, the leaves, and the bud of coconut palms, and to be usually fatal. This is not the place, however, to discuss the many problems of its morphology, ecology, pathogenicity, etc., but its known distribution is most interesting: British Honduras, Panama, Venezuela, Trinidad, Tobago, Grenada, British Guiana, Brazil, Barbados, and Honduras.

In the teasel actually all parts of the plant are invaded—the roots, stems, leaves, flowers, and seed. In most forms of nematosis of plants, organ infections are the rule: primarily of roots, tubers, corms, bulbs, or rhizomes, and next in frequency, of leaves, flowers, seed, etc. These are the conditions most widely seen in the American Tropics.

Tissue nematoses are, for example, the invasions of *Pratylenchus* and *Hoplolaimus* in the parenchyma of roots, and are of wide occurrence in our Tropics. Intracellular infections are rare, and have been observed only in

[4] Note by junior author: In the late Dr. Steiner's notes, this 1915 description of Cobb was given status as a new species, in order to separate it from that of Cobb, 1893. Because Dr. Steiner's manuscript notes appeared to be incomplete it seemed unwise to give here the name he had chosen for the species.

the case of *Radopholus* in plantains. They are here reported and illustrated for the first time (fig. 5).

The present subject is not one of classification only, but has its as yet unknown physiological background.

ROOT KNOT ON COFFEE

The problematical aspect of the root knot nematode attacks on coffee as described by Göldi (1887) and various later authors appears evident. *Meloidogyne exigua*, as observed by Göldi, acted as an extremely virulent agent. It is stated that, in some instances, coffee trees perished almost from one day to the next. This is a virulence quite unknown for root knot types. Furthermore, Göldi's figures, if correct, demonstrate his species with a pharynx (oesophagus) not known in other *Meloidogyne* species. We refer to his figures 15 (a,b,c), 16, and 25, which show bulbous swellings of the precorpus, the pharyngeal portion cephalad of the middle bulb.

Fawcett (1915, p. 28), in discussing root knot as the cause of disease of coffee in Puerto Rico—referred to the organism under the name "*Heterodera radicicola*"—stated: "No real evidence that the trees are really injured by this disease has been noticed. The characteristic swellings caused on roots by this worm may sometimes be seen on the fine roots near the surface. The heavy nature of most Porto Rican coffee soils no doubt prevents it from becoming the pest which it sometimes is elsewhere." Fawcett also mentioned a rather unusual mode of root knot infection, at the base of the tree trunk under the roughened bark. He spoke of seeing the white female bodies of the nematode even up to 1 foot aboveground, and showed a photograph of such a diseased trunk. This is, of course, all very unusual. At the present time we have never reobserved these symptoms.

W. Nowell (1923, p. 229–30) referred to alarming accounts from Brazilian plantations and to their being considered:

> as a serious pest of coffee in Guadaloupe and Martinique. The accounts which have appeared from each of these localities suggest very strongly that the effects described may be largely due to fungus root disease with the symptoms of which they are in close accord. This impression is to some extent borne out by Fawcett's remarks concerning the status of the parasite on coffee in Puerto Rico. Although *Heterodera* is often active there in trees suffering from root disease, no good evidence has been found that the trees are injured by it to any extent, and its presence is not a necessary accompaniment of root disease. The effect of the same parasite on coffee in the German African Colonies was reported to be trifling and easily balanced by the use of suitable manures.

Thus I do not consider that the identity of this species is at present properly established. The region of the State of Rio de Janeiro, Brazil, where this pest occurred, has never been studied since, either as to the species of root knot nematodes involved or as to other plant-attacking forms.

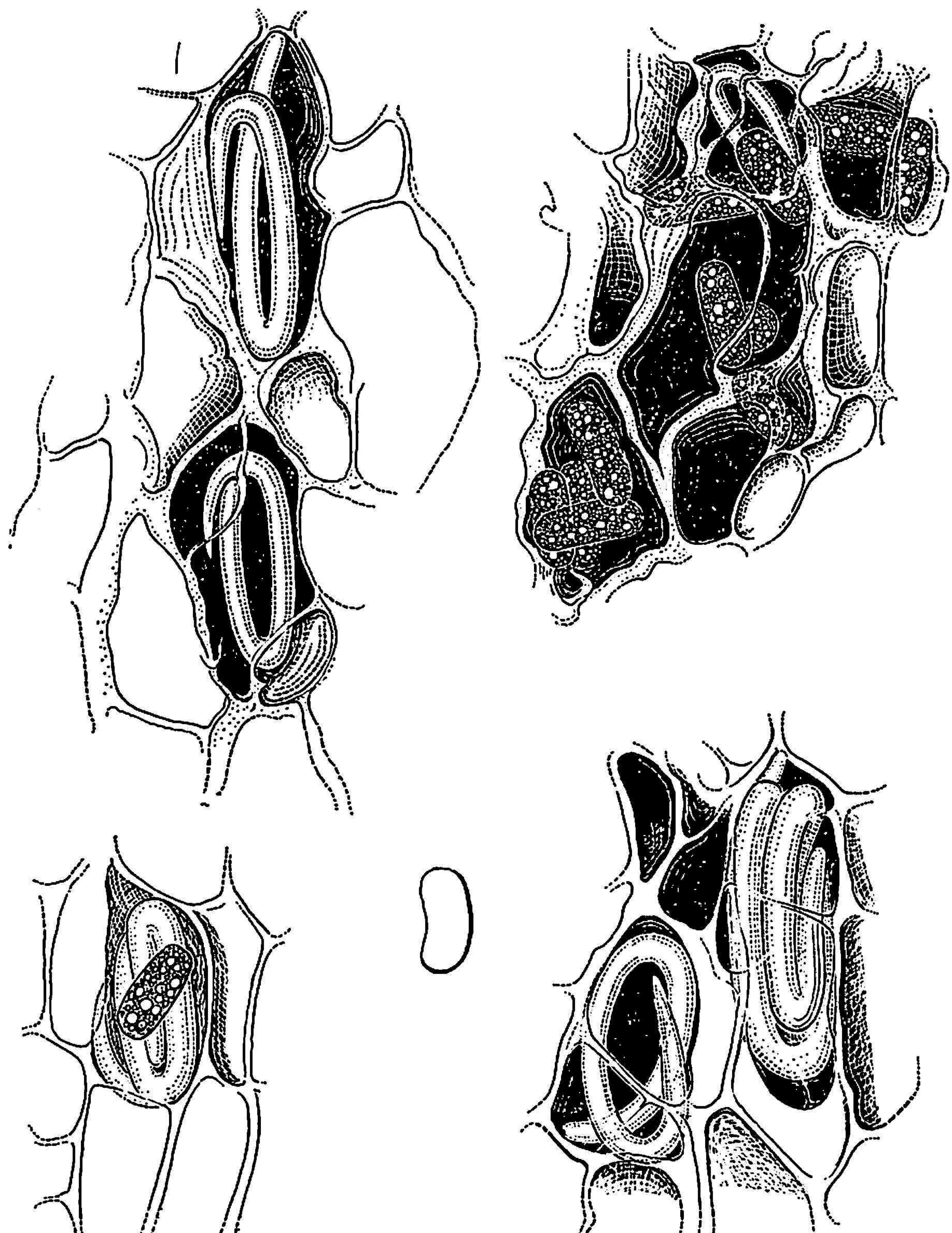

FIG. 5.—Intracellular infections of *Radopholus similis* in banana roots from Jamaica, showing various stages of the nematode from egg to adult. Drawing by the senior author.

Personally, I[5] had first observed root knot on coffee that had been collected, on my request, in the New York Botanical Garden in 1928. It is this material that was studied by B. G. Chitwood and interpreted to represent Göldi's *Meloidogyne exigua*. However, information did not suggest a virulence comparable to that observed by Göldi and by Jobert (1878). In Puerto Rico we have observed root knot on coffee in a number of plantings but, although of pronounced pathogenicity, not of the mentioned virulence. Root knot has been reported on coffee in other regions of the American Tropics but in no instance of the economic importance of the 19th century reports.

The problematical aspect of root knot of coffee extends outside the American Tropics as well. Around the turn of the century Zimmermann, an excellent observer, recognized that two other types of nematodes were most serious pests on coffee in Java: *Tylenchus coffeae* Zimmermann 1898 (now *Pratylenchus coffeae* (Zimmermann, 1898) and *Tylenchus acutocaudatus* Zimmermann 1898 (now *Radopholus similis* (Cobb, 1893) Thorne, 1949). But as much as he emphasized the pernicious character of these two forms, he did not find root knot to be a serious pest of coffee. In fact, he found that root knot which badly infected a weed (*Ageratum* sp.) occurring in Arabica plantings did not transfer to this host, nor did it do so in experiments. Later, in reporting on the occurrence of root knot on coffee in East Africa, he concluded that root knot in this instance did not cause much trouble.

THE PROBLEM OF PLANT NEMATODES IN PRE-COLUMBIAN NEW WORLD AGRICULTURE

It is considered highly probable that one of the most detrimental nematode plant pests, the golden nematode of potatoes (*Heterodera rostochiensis* Wollenweber, 1923) originated in the high Andean regions of Argentina, Bolivia, Peru, and adjoining countries, where also its main hosts, the potato and tomato, appear to have originated. This raises a number of interesting questions, one of which is the presence of nematode problems in early agriculture.

If these geographical regions are the gene center of potatoes and tomatoes, what of the nematodes that attack them in their home region? Are we to look in these regions also for the gene center of this nematode and others of its kind? The casual finding of *Heterodera leptonepia* G. S. Cobb and A. L. Taylor, 1953, a close relative of the golden nematode, in potato material from Peru points to possibilities in this direction. That the Incas in their potato culture followed a rule of not planting potatoes on the same land for several successive years strongly suggests that this was their way of

[5] The senior author.

controlling and living with the golden nematode. Thus it is likely that this pest, and possibly other plant nematodes, were already a problem in this early agriculture. The Maya and Aztec agricultures also appear to have had crop nematode problems; H. Goffart (1958) recently discussed the possibility of nematode pests as a primary cause of crop failures among the Mayas.

RESISTANCE

Little work has been published concerning tropical plants that are resistant and immune to the various nematode noxae. Field observations by Dorothy Chapman in Guatemala confirm particularly the resistance (immunity?) of the crotalarias to root knot; see her list of susceptible plants and those not found attacked on three *fincas*. Unfortunately the species of root knot nematodes occurring in the area of her survey are not known. Her work, however, suggests an avenue for exploration of the possibilities of much economical value to growers.

In Puerto Rico *Cajanus cajan* (L.) Millsp., the pigeonpea, in our experience, is not subject to root knot; at least we have not yet seen an infection under conditions where susceptible plants were attacked. In Hawaii, however, it has been seen subject to this disease. At an ornamentals nursery we have seen roots of the African tuliptree (*Spathodea campanulata* Beauv.) growing intermixed with those of *Gardenia jasminoides* Ellis, wherein the tuliptree was entirely free of root knot while the gardenia was seriously knotted.

EFFECTS OF FERTILIZERS, MANURES, COVER CROPS, AND SIMILAR SOIL AMENDMENTS ON THE PLANT-NEMATODE COMPLEX

In applying fertilizers, and in dealing with them scientifically, only their effect on the crop or plant is usually considered, and therefore only the matter of their food value. Rarely is a thought given to their effect on the nematodes and other biota, with the possible exception of soil bacteria. Here again we are confronted with one-sidedness. I have pointed out earlier in this paper that nematodes are aquatic organisms, and that plant nematodes need moisture to live and to move. It was also mentioned that soil moisture, or soil water, is actually a salty moisture and a salt solution of very diverse composition and changing concentration. All agents and factors that affect this solution doubtless also affect the soil biota, including their nematode component.

Under natural, undisturbed conditions, changes, as they are made by man through soil amendments (fertilizers, liming, pesticides, etc.) simply do not occur. As man began to apply such soil treatments, their effect on nematodes and other soil organisms must have come into play, but little of their nature is actually known. It is a phase of fertilizer studies up to the present time almost completely ignored. Certainly compounds like liquid ammonia, sulfate of ammonia, superphosphate, potash, and others must be detrimental to many of the life forms in croplands, and actually have been shown to exist. Again, exact facts are lacking. Animal manures in solid and liquid form are known in a general way to affect the nematode fauna of treated soils and vegetation, both qualitatively and quantitatively; knowledge is lacking, however, on their effect upon specific plant-parasitic and plant-pathogenic forms.

SUMMARY

This article deals with the nematode problem of the American Tropics, and is a compilation of the late Dr. G. Steiner's notes by Edna M. Buhrer.

According to Steiner, the apparent rapid exhaustion of tropical soils under cultivation is not a depletion in mineral and organic elements, but a condition in which the world of organisms which these soils harbor, particularly nematodes, plays an important part. In spite of the importance of these organisms, very little attention has been given to them.

The presence of nematodes in all agricultural lands, and wherever plants grow and vegetation occurs, is an established fact. This has been shown for such crops as pineapple, sugarcane, and others. Since early years the shifting of cultivation has been practiced in the American Tropics. Although its effects have been almost completely overlooked, now its significance is known as a means of reducing and avoiding the effect of soil pests, particularly of noxious nematodes.

Ecologically speaking, nematodes do not occur in assemblies of a single taxon. Normally there are different types involved which respond to the environmental conditions that surround them. This is why plant-nematode problems are to be studied and acted upon on the basis of the entire ecological situation and not only on that of isolated single noxious nematode types.

Parasitism of nematodes on plants is highly gradated and diverse. The gradations may spread from an unnoticeable impairment of the host to extreme pronounced injury. The disease-producing effects of parasitic nematodes are not accounted for by nutrient depletion alone, nor by mechanical injury or interference, but more importantly by the physiological disturbances created on the host by the injection of digestive compounds by the nematode.

Parasitic nematodes fall into two categories: endoparasites and ectoparasites. In both groups there are sedentary and migratory forms. Both forms, especially the ectoparasites, are dependent on the moisture content of the soil. Changes in this moisture content as well as variations in the

components of the soil solution greatly affect the nematode population. It is unfortunate that there exists almost complete lack of information as to how manures, fertilizers, weedkillers, soil amendments, and pesticides affect plant nematodes and other soil biota.

Plant nematodes have developed some remarkable modes of parasitism, phenomena that deserve attention as curiosities among biological systems. In this article those modes of parasitism are discussed for *Meloidogyne*, *Rotylenchulus*, and *Radopholus*.

Discussed here is also the problematic aspect of root knot on coffee. In this case reports of such observations in which root knot-infected coffee trees perished almost from one day to the next, and root knot nematodes infecting the stem of coffee trees up to 1 foot aboveground have never been reobserved.

It seems possible that the golden nematode and other plant nematodes were already a problem in early agriculture. The proof for this is that the Incas followed a rule of not planting potatoes on the same land for several years. Similar nematode problems seemed to have occurred in the Maya and Aztec agriculture.

Resistance is undoubtedly an important aspect in nematode control. However, very few observations have been reported of tropical plants resistant to certain specific nematodes. Some examples of plants which have never been observed infected by root knot nematodes are crotalarias, pigeonpeas, and the African tuliptree.

RESUMEN

Este artículo trata sobre el problema de los nemátodos en la América tropical, y es una compilación de las observaciones hechas por el fenecido Doctor Steiner, preparada por el más joven de los autores.

Según Steiner, el rápido y aparente empobrecimiento de los suelos tropicales bajo cultivo no es un agotamiento de sus elementos minerales y orgánicos, sino una condición en la que la multitud de organismos que los habitan, particularmente los nemátodos, desempeñan importante papel. A pesar de la importancia de estos organismos, se les ha prestado muy poca atención.

La presencia de nemátodos en las tierras cultivadas y donde hay vegetación, ya es un hecho conocido. Se ha demostrado que es así en el caso de la piña, la caña de azúcar y otras cosechas. Desde los comienzos de la agricultura ha sido la costumbre en la América tropical no sembrar en el mismo terreno consecutivamente. Y aunque casi se han pasado por alto los efectos de esta práctica agrícola, ahora se comprende su importancia para disminuir y evitar los efectos de las plagas de los suelos, particularmente los nemátodos.

Desde el punto de vista de la ecología, los nemátodos no se encuentran

en congregaciones de un solo tipo. Normalmente, hay diferentes tipos que responden a las condiciones ambientales que los rodean. De ahí que se estudien los problemas de los nemátodos perjudiciales a las plantas y se tome acción sobre ellos, no sólo a base de tipos aislados y particulares sino de la situación ecológica en su totalidad.

El parasitismo de los nemátodos en las plantas es gradual y diverso. Los daños pueden variar de apenas perceptibles a extremadamente severos. Los efectos patológicos causados por los nemátodos parasíticos no se deben del todo al agotamiento de los nutrimentos, ni a lesiones mecánicas o entorpecimiento del crecimiento, sino en mayor grado a las perturbaciones fisiológicas producidas en la planta hospedadora por los compuestos digestivos que les inyecta el nemátodo.

Los nemátodos parasíticos caen dentro de dos categorías: los endoparásitos y los ectoparásitos. En ambos grupos hay formas sedentarias y migratorias. Ambas formas, especialmente los ectoparásitos, dependen del contenido de humedad que tenga el suelo. Los cambios de humedad, tanto como la variación en los componentes de la solución del suelo afectan grandemente la población de nemátodos. Es de lamentarse que se desconozca casi por completo el efecto que tales factores como el estiércol, los abonos, yerbicidas, compuestos para corregir los suelos y pesticidas, tienen sobre los nemátodos y otros organismos del suelo.

Los nemátodos parasíticos han desarrollado extraordinarios modos de parasitismo, fenómenos que merecen nuestra atención siquiera por lo que tienen de peculiar dentro de los sistemas biológicos. En este artículo se discuten los distintos modos de parasitismo en los géneros *Meloidogyne*, *Rotylenchulus* y *Radopholus*.

También se discute el aspecto problemático de la presencia de agallas en el árbol de café. En este caso no se han repetido informes de observaciones hechas en cafetos infectados que han muerto casi de un día para otro y de nemátodos de agallas que se encontraron infectando el tallo de árboles de café hasta una altura de 1 pie.

Parece posible que el nemátodo dorado y otros fito-nemátodos hayan sido un problema para la agricultura desde sus comienzos. La prueba de ello es que los Incas tenían la costumbre de no sembrar papas en el mismo terreno por varios años consecutivos. Problemas similares parecen haber confrontado los Mayas y los Aztecas en su agricultura.

Indudablemente, la resistencia de las plantas es un factor importante en el control de los nemátodos. Sin embargo, muy pocas son las observaciones que se han informado sobre la resistencia de plantas tropicales a ciertos nemátodos específicos. Como ejemplos de plantas que nunca se han observado infectadas por los nemátodos de agallas pueden citarse las crotalarias, el gandur y el tulipán africano.