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The red ring-little leaf syndrome in oil palm and coconuts

Carlos Ml. Chinchilla[1]

Introduction

The most important disease of oil and coconut palms in Central America is caused by the nematode *Rhadinaphelenchus cocophilus* : losses of 5-15% in plantations of both palms have been rather common in several countries of Tropical America. In Costa Rica, this disease was reported for the first time (in a coconut palm grove near a commercial oil palm plantation) in the Quepos region in 1977 (Salas 1980). Infected palms were also found in the Atlantic coast during this study. In 1979, the disease was determined to be established in coconut palms along the Pacific coast, from Guanacaste to Golfito (Salas, 1980). Oil palms showing typical symptoms of the red ring disease were found for the first time in Quepos, Costa Rica, in 1984 (Luchini, unpublished data). In Honduras, the nematode was found around the mid seventies in coconut palms located near oil palm plantations in San Alejo, in the localities of La Lima, Chotepe, Puerto Cortés, La Ceiba and Guaymitas (Salas, 1979, unpublished data).

The symptoms of the ‘little leaf disease’ in oil palm were not recognized as associated with *R. cocophilus* in Central America until 1986 (Chinchilla & Richardson, 1987). Nevertheless, these symptoms were observed since the early eighties, and it is believed that the disease has been present since the beginning of the seventies. About the same time (1980), it was also observed that some oil palm plants showed signs of ‘little leaf’ in plantations in the Pacific coast, but no mention was made as to the age of the plants, nor was the symptoms detailed.

Symptoms in oil palm

One of the characteristics of this nematode is the great variability of symptoms it can cause in the coconut and oil palm plants affected. Generally, only coconut palms over four years of age are attacked (Dao & Oostembrink, 1967), and in oil palms, the disease is more common in plants over 5-6 years of age. Several attempts to infect nursery plants of both species have failed (Malagutti, 1953; Dao & Oostembrink, 1967).

The nematode *R. cocophilus* has been associated with at least three types of symptoms in oil palms in Costa Rica, Honduras and other Latinamerican countries. Nevertheless, any combination of symptoms may occur in a particular infected palm.

1. Classic or typical symptoms

In oil palm, the symptom that is considered as classic is produced when older and sometimes intermediate leaves, turn yellowish and progressively become dry (Fig. 1). These symptoms then advance, affecting younger leaves. The oldest leaves usually break at the petiole, a short distance

[1] ASD de Costa Rica, cmlchinchilla@gmail.com

from the trunk, and the part of the leaf farthest away from the trunk remains hanging down for a long period. When the trunk of these palms is cut transversely, a brownish, pink, rose or beige ring, a few centimeters in width and located near the periphery of the trunk, may be seen (Fig. 2-C). In some cases, the ring is not continuous throughout the length of the trunk, and it may appear at the top third of the trunk, but it is apparently nonexistent at its intermediate region, although it may reappear at the bottom part. The ring may also be evident in a small section of the top or bottom parts of the trunk (Fig. 2-D,E). Generally, the new leaves are of a yellowish pale green color and shorter than usual. Nevertheless, when the palm has been attacked severely by the palm weevil (*Rhynchophorus palmarum*), the apical region is partially destroyed. Once the plant is infected, the palm may die in 2-3 months.

Fig. 1. Classical symptoms of the red ring disease in oil palm

2. Little leaf symptoms

Another symptom observed is the condition known as "little leaf", where most leaves preserve their green color and no type of necrosis is present in the stems of the affected palms. Initially, the plant starts producing very short leaves and the center of the crown takes a compact appearance. Eventually, as new short leaves are produced, which may be simple stumps, the central part of the crown takes the appearance of a funnel. As the disease progresses, all new leaves issued are short and deformed, showing different degrees of necrosis of the leaflets, and abnormal degrees of suberization of the rachis (Fig. 3-C). The production of small leaves as another symptom caused by *R. cocophilus* has also been described in Surinam, Brazil and Venezuela (Malagutti, 1953; Van Hoof & Seinhorst, 1962; Schuiling & Dinther, 1981).

The largest population of nematodes is usually located in the young leaves, during their stage of rapid elongation (negative leaves -11 to -2), and they frequently appear in greater numbers in the leaflets of the central and apical parts of the leaf.

Fig. 2. Internal symptoms in oil palm trunks affected by the red ring disease

These leaves, when issued, present a necrosis (drying) of the leaflets much more generalized around the central and/or apical parts, which corresponds to the zone where the greatest population of nematode is located. These leaflets, besides being partially necrosed, do not open completely and remain partially folded along the rachis. Active nematodes were located in leaves as young as those in position -25 to -28. Many nematodes in these negative leaves appear to have a semi-ectoparasitic behavior.

While the disease is progressing, all new leaves in the plant are small and deformed, which makes the plant appear as a giant duster (Fig. 3-B). In cuts from the petioles and rachis of the infected negative leaves, many yellowish-orange spots may be seen. At the zone immediately below the main meristem, dispersed yellowish stains may also be seen.

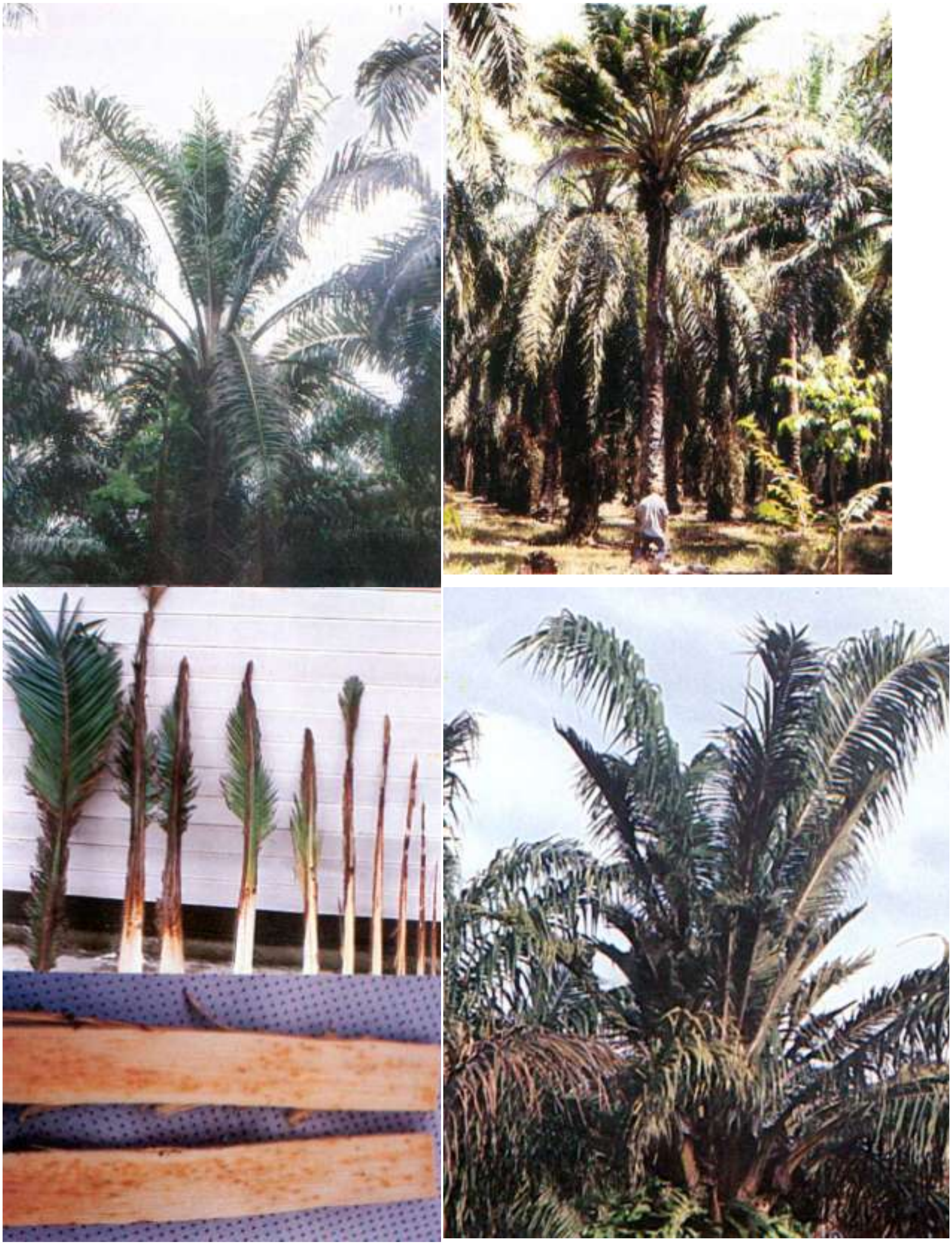
The disease presents itself chronically, and the palm may remain in this condition for several years. A very low percentage of the plants recover, producing some normal-sized leaves. Nevertheless, most of these palms become diseased again, and they initiate a new cycle of small-sized leaf production. The disease causes a pronounced retardation of the longitudinal growth of the stem, wherefore, the palms which have been diseased for three or more years are notoriously shorter than their healthy neighbors.

The inflorescences in development in the leaf axis abort. When the plant has bunches already formed at the time of the first symptoms, these continue their development, but, as the disease progresses, bunch failure invariably makes its appearance. In some of these palms, when their trunk is cut near the base, necrotic dark brown, almost black spots, and (sometimes) a similarly-colored ring more or less defined, may be seen. Generally, this ring only takes up a very limited portion of a longitudinal section of the stem. Kraaijenga & Ouden (1966) observed in some coconut palms, in Surinam, that the symptoms of ‘little leaf’ were not always associated with the development of the red ring in the trunk, and they proposed, as an explanation for this behavior, the age of the studied trees as the responsible factor. In oil palm, it is evident that age is not involved in the development of a particular type of symptoms.

The presence of small leaves must not be taken as the sole indicator *for R. cocophilus* infection, as there are other causes that may bear forth this symptom. Among these causes are: recovery after an attack of common spear rot, *Fusarium* wilt, attack at the whorl region by some insects, boron deficiency, etc.

Maas (1970) in Surinam performed several controlled inoculations in oil palm, and observed that the disease was lethal only in very vigorous plants. Less vigorous plants developed the ‘little leaf’ symptoms. This type of relation is not apparent in Central America, where the ‘little leaf’ symptoms were developed, regardless of the apparent vigor of the attacked plant.

Plants with ‘little leaf’, five or more years old, are frequently observed as a consequence of an attack of Common spear rot and, in some of these cases, the presence of small leaves is a sign of recovery of the diseased plant. Nevertheless, many of these plants will never produce normal leaves again, but will enter a chronic phase of the ‘little leaf’ disease. It has sometimes been observed that there are cases where a previous ‘common spear rot’ attack attracts the weevil, which in turn inoculates the plant with the nematode.



Fi. 3. Little leaf symptoms in oil palm

When the infection by the nematode occurs in a plant with a severe attack of ‘common spear rot’, the plant may or may not show any external symptom that indicates the presence of the nematode. In some rare cases, the shoot of these plants may be totally destroyed, and the plant may even die following the sequence common to this type of disease (Common spear rot), which may occur in 2 or 3 months. When the trunk is cut, the development of a ring or stains, from where the nematode can be obtained, may be seen.

3. Red ring - little leaf symptoms

A combination of the symptoms described earlier, can be seen when the younger leaves are of a pale green color, shorter and more erect than usual, and appear forming a compact mass (Fig. 3-A). The primordial inflorescences are necrosed and the bunches in formation start to rot, or else are small and of irregular ripening. Some of the youngest leaves are extremely small, or are reduced to mere stumps, and the leaflets present different degrees of a necrosis that develops starting from the tips, especially in the leaflets located in the central part of the leaf (Fig. 3-C). Often, some small leaves will not present apparent necrosis, but an arching of the rachis near the apical end. The oldest leaves may remain green for a long time, but a yellowing of the intermediate leaves will eventually occur, and the symptoms will become generalized, thus causing the death of the plant.

In a lengthwise cut, the rachis of the youngest leaves, especially the negative ones, presents a yellowish-orange tinge that increases its intensity after the cutting is performed (Fig. 3-D). Some of the intermediate and lower leaves-petioles show necrotic dark brown stains in their internal parts (Fig 1). Palms that present this symptomatology often develop an intense orange coloration in the external part of the petioles of the older leaves, but similar types of colorations are also observed in plants with nutritional problems.

When the trunk of these palms is transversally cut, different types of internal necrosis can be seen. Depending on the section of the trunk in which the cut is performed, one or more discontinuous concentric rings, or small necrotic spots without a definite distribution pattern, can be seen (Fig. 2-E,F,G,H). Sometimes, the central part of the trunk is occupied by a dark brown or yellowish necrosis several centimeters in radius with a darker brown border. This symptom probably results from the death of the tissues within the ring. In severe cases, this central necrosis of the trunk can be found in different degrees of decomposition, degenerating itself eventually into an aqueous and pestilent rotting. The disintegration of the tissues within the ring is frequently present in older palms that have been affected for several years. The disintegration of the tissue within the ring in the stem or trunk was also observed by Maas (1970) in Surinam.

By performing a lengthwise cut on the stem, it is possible to observe why, depending on where the cut was made, the trunk may appear: a) apparently healthy, b) with a defined ring, c) one or more discontinuous rings, d) a necrosed central area, or else e) dark spots within the central region. The development of the symptoms in the trunk may apparently progress upwards or downwards, which makes it necessary in some cases to make transversal cuts in different sections of the trunk in order to be able to observe the symptoms. This lack of relation between the type and extension of the necrosis in the stem and the intensity of the external symptoms in oil palm, was also observed by Schuiling and Dinther (1981) in Brazil, who also noted that the presence of a few internal stains within the trunk did not necessarily imply the posterior development of a ring in this particular tissue. In some occasions, the palms thus affected enter a chronic stage of the disease in which the leaves do not become yellow nor do they disiccated, but the tree continues producing little leaves for three years or more.

4. Symptoms in coconut

In coconut palms, the symptoms are very similar to those described as the typical symptomatology in oil palm (Nowell, 1919; Fenwick, 1968; Salas, 1980; Kastelein, 1987). The trees show a yellowing and progressive bronzing of the leaves, which advances normally from the older leaves to the younger ones, starting from the tips of the leaflets. The petioles of the affected leaves generally break a short distance from the base, and several yellowish leaves or semi-necrotic leaves may remain hanging around the trunk. Parallel to the development of these symptoms, a premature fall of nuts which have not completed their development occurs, plus a necrosis of the inflorescences. Internally, within the petiole of the affected leaves, and even within some apparently healthy leaves, reddish colorations appear. In the root area, the bark turns yellow and then reddish.

When the trunk is cut transversely, a ring of reddish bands can be located near the periphery. In a lengthwise cut, two parallel reddish lines that join at the base of the trunk and end up as discreet stains at the top part may be seen (Blair, 1970). A reddish central area can also be found without being able to distinguish a ring in the transversal cut at all.

External symptoms of the disease may be indistinguishable from those presented by palms of certain origins attacked by "sudden withering" (Kastelein, 1987). Another symptom, less common in coconut (at least in Central America), is the production of small leaves with different degrees of necrosis of the leaflets. Plants with these symptoms may or may not present the reddish tissue ring inside the trunk. Trees thus affected may live on for years or die rapidly (Nowell, 1919).

Distribution and incidence

In Costa Rica, the symptoms of ‘little leaf’ in oil palm are common, but are prevalent in Honduras, where the typical symptoms of ‘red ring’ are less frequent. As much in Costa Rica as in Honduras, the symptoms considered as classic of ‘red ring’ in coconut palms are very common.

The disease associated with *R. cocophilus* is considered potentially one of the most serious threats to oil palm in Central America, and it is generalized enough in adult plantations. In general, within areas of young palms (belonging to the age group 10 years and under), it is found that the disease is not that common, (0.1% diseased palms/hectare or less) and in older areas (20 years) it normally does not progress much. Nevertheless, the incidence of diseased plants may be elevated in areas 11-16 years of age. Due to the fact that in most cases the genetic origin of the older plantations in Central America is not known, it is not possible to characterize genetically the more susceptible progenies. The biggest increase in the incidence of the disease occurred in

Honduras, specifically regarding some material brought in directly from Africa and planted between 1973-1974. Some of these lots have 10-20% diseased palms in some specific areas.

The vector, *Rhynchophorus palmarum*

The adults of the palm weevil *Rhynchophorus palmarum* L., Coleoptera: Curculionidae) present an ample variation in size, ranging from 20mm. to 41mm. in length (body length determined from the last abdominal segment to the anterior part of the head, excluding the rostrum). The mean body length may depend on the area where the insect is collected: 34 mm in Costa Rica and 31 mm in Honduras (Chinchilla et al., 1991; Morales and Chinchilla, 1991).

The sexes may generally be differentiated, the male bearing a pubescent tuft over its rastrum. This characteristic, nevertheless, can not be used with the smaller specimens (usually less than 29 mm) as it is absent in the male. The separation of sexes must be made, in these cases, checking the genitalia.

Depending on the type of trap used to capture the adults in the field, there may be a prevalence of males or females. When pieces of oil palm stems were used more males were captured, but in field trials with the aggregation pheromone of the male, more females were obtained. Nevertheless, in all studies, mean body length in males was larger than in females. The life cycle, from egg to adult, occurs within 80-160 days and the adult may live for three months. In coconut palms, egg-laying occurs at the axillas of the leaves, directly on the trunk, where the female deposits 10 to 48 eggs daily within a period of 8-10 days. Both the mating period and the egg-laying period occur within 14 days (Griffith, 1968). According to Hagley (1963), approximately 73% of the eggs were fertile. The ovoposition period takes 9-11 days; some females lay up to 60 eggs, during the first three days. Copulation may occur between insects recently emerged from the pupa, and takes about 3 minutes. Egg hatching occurs in 3 days, and then follow 9 larval stages (60 days), a pre-pupal stage, and finally the pupal stage. Adults are more active early in the morning and late in the afternoon.

The importance of *R. palmarum* as a primary pest of oil palms is sometimes questionable, and it is generally found attacking palms that have been physically injured (tools, rat attacks, etc.), or have been affected by some type of disease that causes fermentation of the tissues, as is the case of Wet Basal Rot and Common Spear Rot. The development of a high number of larvae within these plants may aggravate the disease symptoms and accelerate the death of the palm. In the case of the spear rot in adult palms, where the population of *R. palmarum* is elevated, the insect invades the shoot of the affected plant and, depending on the number of larvae, may cause the death of the palm without allowing the problem to be detected in time. In coconut palms, *R. palmarum* itself constitutes an important pest, and a population of thirty larvae per palm is probably enough to cause its death (Fenwick, 1967; Griffith, 1968, 1969).

Natural enemies

Very few studies have been done on the natural regulating factors of the different stages of the life cycle of *R. palmarum*. It is known that elevated populations of larvae found in a trunk provoke cannibalism. Also, a high mortality rate in larvae is produced after the attacked tissue begins to rot. Some lizards, and perhaps toads, feed off the adults. In Trinidad, Griffith (1969b) found that a bacteria *Micrococcus* sp. attacked larvae, causing their death in a few days. It is also known that the nematode *Neoaplectana* sp. destroys the adults, pupas and even larvae of the insect (Blair, 1970).

The nematode *Rhabditis* sp. has been found to multiply saprophytically in decomposing diseased coconut palm tree tissue, and it is then acquired *by R. palmarum* , adversely affecting its longevity (Griffith, 1968). Another nematode, *Praecocilenchus* sp, is considered a true parasite of *R. cocophilus* (Nickele, 1974, Morales & Chinchilla, 1991).

Causal agent of the disease

The causal agent of the disease seems to be the nematode *R. cocophilus*. This is a nematode approximately 1 mm in length, very slender and transparent. Its life cycle comprises an egg stage and four larval stages. The complete life cycle from egg to adult is one of the shortest in the animal kingdom, occurring in only 9-10 days (Blair & Darling, 1968).

It has been observed that the nematodes associated with the ‘little leaf’ symptoms in oil palm, differ in several morphological characteristics from those associated with the typical symptoms in coconut palm. The greatest difference between populations is the length of the nematode, which is greater in specimens from coconut palms (Salazar & Chinchilla, 1988). These morphometric differences may well represent only infraspecific variability (Giblin-Davis, R. *et* al., 1989).

Location of the nematode within the palm, within the vector and in the soil

Most studies on *R. palmarum* and *R. cocophilus* have been performed in coconut palm. In this palm, the nematode is located in the reddish tissue of the ring inside the trunk, and immediately adjacent to the ring, especially on the inside. The exact reason for the formation of the reddish ring within the stem has not been fully and clearly explained as of yet (Blair, 1970b).

At the top part of the coconut palm stem, where the tissue is softer, it is possible to find the nematode in discolored areas and in the adjacent tissue; there it is usually found within the intercellular spaces in the parenchyma, or else in cavities formed by the disintegration of the cells of this region (Blair & Darling, 1968; Nowell, 1919; Blair, 1970).

Adult forms and eggs were found in great numbers in the intercellular spaces, at the top part of the trunk, exactly in the zone where the ring turns discontinuous and where discreet spots appear (Blair & Darling, 1968).

Even when the nematode is not located within the xylem, this is obstructed by the formation of tyloses, which impede the free movement of water within the plant (Fenwick & Macharaj, 1963; Blair & Darling, 1968; Hoyle, 1971). Kastelein (1987) found in coconut palms that the greatest number of nematodes was located in the petioles of the older leaves.

In oil palms with ‘red ring’ symptoms in the stem, the nematode is also located in the discolored tissue and within the internal adjacent tissue, which is still apparently healthy. Nevertheless, it is common to find the nematode absent from the trunk, especially where necrotic discrete spots are present, which could indicate the failure of the nematode to establish itself completely within those tissues. Inside the ring area, Schuiling and Dinther (1981) found that the concentration of the nematode could vary between nil and 4833 per gram of tissue and most of the individuals were found death or dying. The nematodes could not be obtained from the trunks of several plants that showed other symptoms. In general, in the necrotic tissue of the petioles, the concentration of nematodes was greater (20-8400 per gram of tissue) and the number of dead individuals was smaller. The number of nematodes per gram of infected tissue in coconut palms may be as high as 11000 (Blair, 1970).

The nematode has never been located in the peduncles of the inflorescences in coconut palms (Blair & Darling, 1968). Schuiling and Dinther (1981) could not find the nematode in the petioles of the older leaves of diseased oil palms in Brazil, wherefore the authors discarded the possibility of transmission during leaf pruning.

The number of nematodes found at the roots and in the soil around diseased trees is generally very low or none at all (Kastelein, 1987). This author found a quantity of nematodes between 0 and 20/100 g of soil in the area around infected coconut palms. The nematode was located as deep as 80 centimeters, but most of them were 30-40 centimeters deep in the soil. During the rainy season, the nematodes were located nearer the soil surface.

Fenwick (1962) found that the infection of the roots persisted for almost a year at the sites where the trunk of a diseased coconut palm had been excavated. This information is not compatible with the findings of other authors, who informed of a survival of the nematode in the soil for 2-3 days, and 90 days in decomposing infected tissue (Griffith, 1978; Esser, 1986). Several other studies performed in both coconut and oil palms, have not detected the presence of the nematode in roots and in the soil near diseased palms (Schuilin & Dinther, 1981).

In Quepos (Costa Rica) and San Alejo (Honduras) repeated sampling of the roots and soil adjacent to the palms suffering ‘little leaf’ was carried out, and not one specimen of *R. cocophilus* was found.

Survival of the nematode

Healthy oil coconut and wild palm trees recently felled may be easily colonized by *R. cocophilus* if visited by *R. palmarum* contaminated with the nematode (Maas, 1970). This situation explains why the occurrence of coconut or oil palms with ‘red ring’ is not essential to the survival of the nematode nor for the contamination of the vector. Wild palm trees are frequently felled and the trunk abandoned as a normal practice in Central America (to extract the heart of the palm or to use the trunk or foliage for other purpose).

The most persistent form of the nematode is the third larval stage, characterized by a tapered terminal end of the body. This larval form (0.84 mm) survives in tissues in decomposition for up to three months, during which it may be acquired by adults or larvae of *R. palmarum* . The third larval stage is also present within the vector and it is the infective stage. The nematode does not suffer changes nor does it multiply inside *R. palmarum* , but it can survive the insect metamorphosis (Griffith , 1968).

The nematode may be located inside the intestines, the body cavity and in the excrement of the vector. Externally it can be transported in pieces of infected tissue caught in the hairs of the insect (Hagley, 1963, 1965; Griffith, 1968; Blair, 1970). The nematodes present inside the body of the insect are generally alive and are all the same size; but those that appear on the external part of the vector represent different development stages (Griffith, 1968; Schuiling & Dinther, 1981). Griffith (1968) found in Trinidad that 80% of the adults *of R. palmarum* transported the nematode within the body cavity and all belonged to of the third larval stage. Approximately 67% of the nematodes inside the insect larvae were located in the trachea and the majority were expelled during a molt. Nearly 50% of the nematodes inside the body of the vector survived the molt to adulthood (Griffith, 1969b).

R. palmarum a**s a vector and beginning of the infection**

There is no doubt about the role of *R. palmarum* as an active vector *of R. cocophilus* , but the presence of insects contaminated with the nematode do not necessarily imply the presence and development of the ‘red ring’ disease in coconut or oil palms. Some authors have informed about the disease without the apparent presence of *R. palmarum* within the plantation (Malagutti, 1953; Dao & Oostenbrink, 1967). Kraaijenga & Ouden (1966) found that in Surinam, the insects were frequently infected with *R. cocophilus*, but the disease was rare in both coconut and oil palms, which indicated that the nematode was probably endemic in wild palms. The low incidence of the disease was explained by the presence of a prolonged dry period, which is repeated twice a year in Surinam, and which could be detrimental for nematodes that are transported externally by the vector.

The percentage of adult insects that carry the nematode internally and/or externally varies amply from one place to another and appears to be strongly influenced by environmental conditions and by the quantity of cultivated or wild palm trees that act as reservoirs for the nematode (Table 1).

Fenwick (1967) found that reducing the population of weevils by applying insecticides to the axillae of the coconut palm leaves reduced not only the population of the insect, but the appearance of new cases of the disease as well. Nevertheless, the reduction in the vector population was not always related to a proportional fall in the incidence of the disease. This author did not find a clear relationship between the fluctuations in the population of the insect and the appearance of new cases of ‘red ring’. Other observations indicated that the total amount of insects present in a plantation and the percentage of the insects that were contaminated, were not necessarily correlated with the incidence of ‘red ring’ disease in coconut or oil palms. In Surinam, Maas (1970) found 27% of insects to be contaminated, but the incidence of the disease was extremely low during the study period in 1969. In 1962, Van Hoof & Seinhorst (1962) had found only 7% of insects infected and also a very low incidence of the disease. Considering the incubation period (ca. 3.5 mo.), there might be a close relationship between the fluctuation of the population of the infected vectors, and disease incidence (Morales y Chinchilla, 1991).

Table 1. Percentage of infestation of *R. palmarum* by *R. cocophillus* in several countries

Percent	Type of contamination	Location	Observations	Reference
38.5	external	Trinidad	Up to 71 nematodes /insect	Hagley, 1963
50.0	External + internal	Trinidad		Cobb cited by Hagley, 1963
72.0	external	Trinidad		Fenwik, 1962
76.0			13% with 50 or more nematodes	Fenwik, 1962
72.0		Grenada		Singh, 1972
3.9		Brazil		Luchini, s.f.
16.3		Brazil	6.1% with 2 or more nematodes	Fenwick cited by Hagley, 1963
40	internal + external			Blair, 1970b
10.9	5 times more internal contamination than external	Brazil	0.5 - 3% insects infected by trap (5 day collect) 40 - 6500 nematodes in adult insects and 50 - 100 in larvae. 16.5 - 28.1 number of adult insects per trap in five days	Schuiling & Dinther, 1981 Kastelein, 1987
1.76	Internal + external	Costa Rica	Population peak in the dry season. Higher % of contaminated insects, last months of rainly season	Morales & Chinchilla
30-68	Internal + external	Honduras	Population behabior like in Costa Rica. Most insects trapped in palms of intermediate age.	Chinchilla, *et al* , 1991.

There is still a fair amount of controversy on the form of contamination of a healthy oil palm by the nematode. The fact that the disease in coconut palms is more common in low and poorly drained areas, and that the nematode may be found in the root area and in wet soil, induced several authors in the past to suggest a possible root transmission of the nematode. This possibility was supported by the fact that the inoculation of one sole root caused the development of the typical symptoms in an originally healthy tree (Fenwick, 1968).

Hagley (1963) found that the contamination with the nematode by means of *R. palmarum* in coconut palms occurred especially in the softer crown tissues, near the axillae of the leaves. The acquisition of the nematode by the vector was influenced by the concentration of the nematodes in the tissue and only the more active nematodes were easily acquired by the insect. Other factors that affected the acquisition were the antecedents of the feeding habits of the vector; insects that had first fed on healthy tissue were not contaminated with the nematode when fed later in infected tissue. Moreover, in those insects that had been continuously feeding on healthy tissue and then placed on infected tissue, the nematodes that were thus acquired were adversely affected and some were found dead inside the body of the vector. When adults of *R. palmarum*, recently emerged from a pupal stage, were fed on infected tissue, the internal acquisition of great quantities of nematodes could be seen. This situation could explain, in part, Griffith's observation (1974) that the first recently emerged adults from a diseased coconut palm always carried more nematodes than the insects that came out of the tree after the crown had entered a state of advanced decomposition, where the nematodes were probably not very active and their concentration in the tissues had been reduced.

The infection may be artificially induced in coconut palms by means of a suspension of nematodes or of a piece of diseased tissue placed at the crown or at the foot of the plant, with or without mechanical damage to the roots. Infection can also be induced by way of the axillae of the leaves, at the petioles, or by placing the nematode directly in the trunk (Dao & Oostenbrink, 1967; Blair, 1970b; Blair & Darling, 1978). The infection that is naturally induced will probably, and frequently, occur in coconut palm trees by way of cracks and/or wounds in the trunk near the axillae of the leaves (Blair & Darling, 1968; Blair, 1970b; Griffith, 1978).

Griffith (1978) concluded that few nematodes could be effectively transmitted by the weevil while they feed, but an elevated percentage of infection (72%) was obtained by means of the confinement of contaminated insects within the internodal zone in the crown of healthy coconut plants. The infection here could have begun during the feeding process, during egg-laying or by nematodes externally carried by the insect or transferred through their excrement (Hagley, 1963; Blair, 1970; Griffith, 1978; Schuiling & Dinther, 1981).

The presence and development of the symptoms in the stem were not related to the site of inoculation of the nematode nor to the development of the external symptoms. Blair (1970) inoculated coconut palms in the basal bulb area and in the top part of the stem and observed that the internal symptoms were completely developed before external signs of the disease appeared. A similar behavior was observed by Schuiling & Dinther (1981) in oil palm. Signs of internal infection included the formation of the ring inside the stem, the discoloration of the bark of the root and of the petioles. The presence of an ascending or descending ring within the trunk did not depend on the site of inoculation of the nematode (Blair, 1970).

According to Griffith (1968) the infection by the nematode in coconut could be provoked by several artificial means (by way of the root, direct placement of the nematode in healthy tissue, etc.) but the only "natural" method of infection was through the internal implanting of nematodes within the tissue of the plant during the process of ovoposition by *R. palmarum* . The author considered that the number of nematodes found normally in the soil (1-4/50 g) and externally on the body of the vector were too low to be able to guarantee a successful infection by way of the root or through the direct implanting of nematodes, externally carried.

Griffith (1968) considered that a minimum number of approximately 50 nematodes in the body cavity of the insect were necessary to turn the insect into an effective vector. The presence of 200 or more nematodes within the body cavity was common, and these nematodes were concentrated in the ovipositor region: hence, they are passed on to the healthy plant during oviposition. According to this theory, *R. palmarum* males can not directly transmit *R. cocophilus* .

Several observations by Griffith (1978) made him conclude that the female insects that measured 30 mm or less were the active vectors of the nematode. Regarding the observed population, only 16% of the adults were of small size, and this reduced proportion of vectors made the progress of the disease relatively slow in the studied area in Trinidad. This ostensibly low proportion of vectors was maintained all along whereas the small-sized insects tended to mate among themselves, thus originating potential vector descendants. Because the population of small males was very reduced (8% approximately), there were, consequently, many small females without an opportunity to find a mate; hence, they could eventually transmit the nematode as they laid unfertilized eggs. This situation produced the sporadic apparition of a coconut palm with symptoms of 'red ring' without the development of *R. palmarum* larvae (Griffith, 1978). The mating of the vectors and the development of their larvae in healthy tissue produced, according to Griffith(1978), adults larger than the ones belonging to the range of the vectors, but that, genetically, continued being potential vectors.

The adult vectors preferably occupied, according to Griffith (1969a), the axillae of the leaves of diseased coconut palms, probably attracted by the smell of decomposing tissue. This preference of *R. palmarum* adults for the axillae of the leaves of diseased plants, has not been documented in the case of oil palms, particularly regarding those with 'little leaf' symptoms, possibly because of the absence of rotting or decomposing tissues.

In reference to the relationship between the size of adults of *R. palmarum* and the level of contamination with *R. cocophilus* , it was not ascertained by Schuiling & Dinther (1981) in Brazil, Singh (1972) in Grenada, Chinchilla et al , 1991, and Gerber and Gilblin-Davis, 1990. Furthermore, we have commonly observed copulation taking place among individuals of very different body size. Enormous differences in size in other types of weevils are common, the most outstanding one being the case of *Rhynostomus barbirostris* , and these differences in size among individuals of the same species are not related as long as we know, to any type of contamination by some other organism.

Griffith (1978) and Singh (1972) found that 97% or more of the coconut palms infected with the 'red ring' disease, also had manifest evidence of the attack by *R. palmarum* , with the presence of larvae and adults of the insect. This situation is sometimes observed in oil palm in Central America. Nevertheless, the development of the symptoms of 'little leaf' without detecting in the diseased tree any sign of the activity of *R. palmarum* , is very common. In these situations, it may be assumed that the infection did not occur during the ovoposition, but by nematodes transported externally by the vector or internally and transmitted during feeding of the insect or by means of the excrement. Infection may well also have taken place during the ovoposition of an infected female in the crown region, where larvae failed to develop and died prematurely, but infection by the nematode persisted.

The evidence accumulated so far implies that the nematode populations that attack coconut palms may also infect oil palm and vice versa. Kraaijenja & Ouden (1966) in Surinam placed pieces of infected tissue from an oil palm with 'little leaf' symptoms, in a healthy coconut palm tree, and they reproduced the typical symptoms of 'red ring' within the trunk. Nevertheless, this tree did not show any external symptom, even 10 months after the inoculation, when it was felled for the observation of the internal tissues. Dao and Oostenbrink (1967) performed crossed inoculations with nematode populations obtained from coconut and oil palm, thus achieving infection in both cases, but these authors are not clear regarding the symptoms obtained in each case. Maas (1970) performed inoculations in the trunk of oil palms with pieces of tissue from the trunk (of a coconut palm?) with the symptoms of 'red ring' and reproduced the symptoms of 'little leaf'; nevertheless, the nematode could not be retrieved from the young deformed leaves of the inoculated plants.

Malagutti (1953) in Venezuela, performed crossed inoculations with populations of nematodes obtained from coconut and oil palm, thus obtaining the development of the typical symptoms of the disease in 80-90 days in both plants. Inoculations performed in one year old palms did not reproduce the disease.

Other palms that may be attacked by *R. cocophilus* are: *Attalea* sp., *Mauritia flexuosa*, *Maximiliana maripa*, *Roystonea oleracea*, *Acrocomia aculeata*, and *Oenocarpus distichus* (Schuiling & Dinther, 1981).

Epidemiology

In coconut palm plantations in Trinidad, it was observed that *R. palmarum* populations declined during the last part of the dry season and the beginning of the rainy season (Hagley, 1963). Apparently, rainy periods would favor the increase in population. The greatest plant losses by the red ring disease occurred at the end of the rainy season and the beginning of the dry season. Assuming a period of incubation of 6-8 weeks, Hagley concluded that there existed a fair correlation between the incidence of the disease and the abundance of the vector. Hagley (1963) assumed that the activity of *R. palmarum* adults had great influence over their capacity as vectors; young insects 2-4 weeks old constituted the majority of the population after a rise in population had begun. Young adults were very active and had great capacity as vectors, and they could cause the majority of the new infections, which would be manifested 6-8 weeks later. Throughout the vector population peak, the greater part of the adult insects were already old (6-8 weeks) and not very active as vectors.

Fenwick (1967) did not find a clear relation between a population peak for *R. palmarum* and an increase in the incidence of the disease 4-5 weeks later. Treating the axillae of healthy coconut trees with insecticide caused a reduction in the population of the vector, but it was not accompanied by a proportional reduction in the incidence of the disease.

In general terms, a fairly clear relation has been observed to exist in coconut palms between the apparition of the symptoms of the disease and the presence of *R. palmarum* in the infected trees. Furthermore, in several studies there has also been a clear correlation between incidence of the disease and the seasonal variation in the abundance of the vector (Hagley, 1963; Blair, 1970; Griffith, 1978; Singh, 1979, Morales and Chinchilla, 1991).

According to Griffith, (1978), the infection cycles in coconut palms occur every three months and, commonly, a diseased tree infects only two other healthy neighboring trees due to the reduced quantity of vector insects that emerge from each diseased tree. The vectors (smaller than 30 millimeters) emerged first, whereas their parents were also the first to arrive at the tree when it was still healthy. Afterwards, other insects, most of them non-vectors, invaded the diseased tree. This hypothesis does not explain clearly, among other things, why there are so few coconut palm trees infected by the weevil without being infected by *R. cocophilus* , since the greater part of the population of *R. palmarum* that continuously emerges from the diseased trees is, theoretically, formed by non-vectors. Griffith (1969a), on the contrary, found that only 3% of the palms attacked by the weevil were not infected by *R. cocophilus* .

Schuiling & Dinther (1981) measured the changes in populations of *R. palmarum* in Paricatuba, Brazil in an oil palm plantation, by means of traps, and they found a negative correlation between the abundance of insects contaminated by the nematode and rainfall: 9.7% contamination in the dry season and 3.9% in the rainy season. Peaks of maximum incidence of the red ring disease were observed approximately five months after the appearance of an increase in the number of insects contaminated with *R. cocophilus* . These five months were considered by the authors as the incubation period of the disease.

In Central America, the *R. palmarum* population associated with oil palm reaches its peak during the dry season and the percentage of insects that carry the nematode is greater during the last months of the rainy season (Chinchilla et al., 1991, Morales and Chinchilla, 1991). A lower proportion of contaminated, field collected adults, during the last months of the dry season, may be the consequence of this being a population of old insects, that have lost most of their nematodes in the environment.

Schuiling & Dinther (1981) did not find evidence of the development of the disease within infection foci in the field and only in 5% of the cases were the affected palms adjacent to another palm bearing the symptoms. The incidence of the disease in the study area was between 0.4 and 6 diseased palms per hectare. In Central America, the most common situation is a uniform distribution of new cases in the plantation. Normally, a group of three or four, non contiguous plants (separated by one or two healthy trees) forms a new foci. Studies performed in Honduras and Costa Rica have shown that the population density of *R. palmarum* in palms 5-6 years old was considerably lower than the population found in areas 10 years and older. Higher populations of the vector in adult palms, are responsible in part of a higher disease incidence in these areas.

In coconut, the highest incidence of the disease has been found in poorly drained soils. This observation seems to indicate a possible transmission by way of the root, but it could also imply that these particular conditions predispose the plants to the attack. On the other hand, under the typical conditions of drought, the disease was maintained at a fairly low level (Fenwick, 1968).

Disease control

Disease control must be integrated and directed as much towards decreasing the vector population, as towards the reduction of the sources of nematodes within the plantation and its surroundings.

A practice used with a certain degree of success in coconut palms, which consists of verifying the presence of the nematode by means of examining a sample taken from the trunk with the help of a drill or borer, is not entirely recommended for oil palms for two fundamental reasons: a) the necrosis in the trunk may be very limited or absent. b) even in the presence of necrosis, the number of nematodes in this area may be extremely low or none at all.

In the case of plants with severe symptoms, it is recommended to poison the plant with a systemic herbicide injected in the trunk, and felling the plant after it has dried. It has been observed that older plants can be easily poisoned with 100 ml of MSMA (Bueno 6), but higher doses are required (125-150 ml) to kill some of the intermediate-aged plants with a vigorous growth rate. A mixture of Picloran and 2,4-D has also been recommended for plant elimination. Even though the insecticide does not kill the nematode directly, it does help interrupt the transmission cycle making the treated palm less attractive to *R. palmarum* . In spite of this unattractiveness, it has been occasionally observed that some palms injected with MSMA were colonized by weevil larvae, wherefore the treated palm should be felled once they are dry, and be checked for the presence of larvae for their elimination. As the tissues rot, the nematode will eventually die.

When a palm is severely attacked by the weevil, it must be felled and cut in sections, which are then cut open lengthwise; an insecticide is then applied, such as Furadan F, Sevin (carbaril), Dipterex (Triclorfon), Lannate (Metomil), Vydate (Oxamil), Nemacur (phenamiphos), Azodrin (monocrotophos), etc. In the case of palms which present symptoms of ‘little leaf’ without extensive necrosis of the trunk, there is, apparently, the possibility of recovery by means of using trunk-injected systemic nematicides, which may be also applied directly in the whorl of the plant. In several preliminary tests, it was observed that products like Carbofuran (Furadan F), Oxamil (Vydate CS) and Fenamifos (Nemacur CE) permitted the apparent recovery from the symptoms of ‘little leaf’ in a percentage of the treated palms. The visible response took around 6-8 months to appear, due to the fact that the young leaves that were affected during their active growth period always came out deformed. The lack of response to the treatment may be due to several factors, but it is obvious that, if there is extensive damage done to the trunk of the palm by the disease, recovery will be literally impossible.

Several treatments with nematicides on diseased coconut palm trees have been largely unsuccessful. The main problem concerns the lack of translocation of these products within the diseased plants, due to the occlusion of the xylem. The incapability of the nematicides of penetrating the trunk zone where the nematodes are, may imply that chemical treatments do not have great possibilities of being truly effective. In healthy plants, Nemacur injected in the trunk and applied to the soil (granulated) was active within the tissues for 30 days and 14 weeks, respectively. A 14-week activity in the plant was also observed for soil-applied Temik. Temik may also be absorbed through the axillae of the leaves. Both Temik and Nemacur presented great insecticidal activity against *R. palmarum* (Hayle, 1971).

In several tests performed on oil palms in Honduras, treatments with soil-applied Temik 10 G (80-200 g/plant), trunk-applied (10 g/plant), and axilla-applied (30 g/plant) for plants with symptoms of 'little leaf', were entirely ineffective. However, when Temik was applied directly to the whorl, some plants seemed to recovered from the little leaf symptoms.

The attraction of *R. palmarum* adults by certain types of recently exposed internal tissues, especially pieces of stem from diverse palm trees, has been used against weevil populations very successfully. Adults that reach these traps may be collected by hand, or else the pieces of tissue may be impregnated with an insecticide such as Lannate, Sevin, Furadan F, Vydate, Nemacur, Dipterex, etc. Pieces of oil palm trunks are generally more efficient as weevil traps than coconut palm trunk pieces (Kraaijenga & Ouden, 1966) and, according to Fenwick (1966) it is better to use pieces of non-infected trees. Traps made with pieces of plantain or banana pseudo-stems, crushed sugar cane stalks, or ripe fruits, are not so attractive to *R. palmarum* (Salas, 1979, unpublished material). Some strong smelling insecticides (i.e. Cytrolane) have a deterrent effect on adults of *R. palmarum* . These insecticides should not be used in traps, but can be very useful to protect the cuts of recently fell diseased palms.

Hagley (1963) found that the application of insecticides at the axillae of the leaves of healthy coconut palms, reduced the incidence of the disease and these treatments were more effective when done during the population peaks of the vector. In general, it has been observed that a reduction in a given percentage of *R. palmarum* populations is not always related to a proportional fall in the incidence of the red ring disease (Hagley, 1963; Fenwick, 1967).

Whereas the weevil is attracted by any type of wounds, these must be avoided at any cost, especially during harvest. Spear Rot must also be given special attention, especially in palms that have entered the stage of susceptibility to the nematode (5-6 years); in these cases, it is advisable to treat the diseased part with an insecticide to avoid risking visits from the vector insect.

Natural recovery of diseased plants and resistance

It has been observed that some plants with the 'little leaf' symptoms begin a cycle of normal-sized leaf production and that, after a certain number of months, they renew all their foliage . In some cases, this "recovery" is temporary and the plant again initiates a little-leaf production cycle. Kraaijenga & Ouden (1966) in Surinam attributed to climatic factors (such as a very prolonged dry season) the fact that some coconut plants recovered, or that some were kept with 'little leaf' symptoms for several years. Van Hoof and Seinhorst (1962) also observed the phenomenon of the apparent recovery of the symptoms of 'little leaf' in oil palms in Surinam. Coconut or oil palms with the typical symptoms of 'red ring' does not recover and the plant invariably dies after a few months.

In Honduras, it has been observed that the nematode may be found in oil palm even in leaves as young as the -25 leaf, which indicates that a natural or induced visible process of recovery could even take a year, in a palm with a rate of foliar emission of 2 leaves per month. Van Hoof & Seinhorst (1962) found the first signs of nematode injury in leaves 2.2 to 4 centimeters long, all of which presented small yellowish patches over the petiole and the base. The nematode was found even in leaves 1.75 meters long with the leaflets still folded and protected from the sun. The authors concluded that the nematode lives in these tissues ectoparasitically. This type of behavior could explain why these nematodes are more susceptible to prolonged dry periods.

There are no concrete studies that show the resistance or tolerance to the disease of coconut, or the oil palm (*E. guineensis* and *E. oleifera*). In the coconut palm, the tolerance to infection by the nematode seems to increase with the age of the trees. Blair and Darling (1968) observed that the infection from inoculations by way of the root, stopped when it got to the bulb area of the trunk in palms over 12 years of age. In palms 4-7 years old, the disease was generalized in two months, whereas the nematode passed from the root to the basal bulb and established itself in the trunk, originating thus the typical symptoms of the disease.

Schuiling and Dinther (1981) observed in Brazil that in some plants, the development of the symptoms was detained immediately after the youngest leaves came out shorter and with a more compact appearance. The oldest leaves remained green and the inflorescences and bunches continued their development. These plants maintained this condition for one year or more, and the authors considered it a tolerance to the nematode. It was also found that the frequency of this type of response was augmented with age.

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